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KARYOTYPE EVOLUTION OF SHREW MOLES (SORICOMORPHA: TALPIDAE)

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The Chinese long-tailed mole (*Scaptonyx fusicaudus*) closely resembles American (*Neurotrichus gibbsii*) and Japanese (*Dymecodon pilirostris* and *Urotrichus talpoides*) shrew moles in size, appearance, and ecological habits, yet it has traditionally been classified either together with (viz subfamily Urotrichinae) or separately (tribe Scaptonychini) from the latter genera (tribe Urotrichini sensu lato). We explored the merit of these competing hypotheses by comparing the differentially stained karyotypes of *S. fusicaudus* and *N. gibbsii* with those previously reported for both Japanese taxa. With few exceptions, diploid chromosome number (2n = 34), fundamental autosomal number (FNa = 64), relative size, and G-banding pattern of *S. fusicaudus* were indistinguishable from those of *D. pilirostris* and *U. talpoides*. In fact, only chromosome 15 differed significantly between these species, being acrocentric in *D. pilirostris*, subtelocentric in *U. talpoid*es, and metacentric in *S. fusicaudus*. This striking similarity is difficult to envisage except in light of a shared common ancestry, and is indicative of an exceptionally low rate of chromosomal evolution among these genera. Conversely, the karyotype of *N. gibbsii* deviates markedly in diploid chromosome and fundamental autosomal number (2n = 38 and FNa = 72, respectively), morphology, and G-banding pattern from those of *Scaptonyx* and the Japanese shrew moles. These differences cannot be explained by simple chromosomal rearrangements, and suggest that rapid chromosomal reorganization occurred in the karyotype evolution of this species, possibly due to founder or bottleneck events.

Key words: chromosome, evolution, karyotype, *Neurotrichus gibbsii*, *Scaptonyx fusicaudus*, shrew moles, Talpidae

Among the 17 extant genera of the family Talpidae, 4 are semifossorial (Hutterer 2005; Yates and Moore 1990). These 4 monotypic semifossorial taxa are located sporadically around the Pacific Rim: the American shrew mole (*Neurotrichus gibbsii*) along the northwestern coast of North America, the lesser (*Dymecodon pilirostris*) and greater (*Urotrichus talpoides*) shrew moles of Japan, and the Chinese long-tailed mole (*Scaptonyx fusicaudus*) in the montane region bordering China, Myanmar, and Vietnam. Despite similarities in size, ecological habits, and outward appearance, the phylogenetic placement of these taxa remains enigmatic. Simpson (1945) classified the family Talpidae into 4 distinct subfamilies, Uropsilinae, Desmaninae, Talpinae, and Scalopinae, and placed *Scaptonyx* and the 3 genera of shrew moles (together with the American fossorial moles) into the latter subfamily. Stroganov (1948) similarly grouped *Scaptonyx* with the shrew moles (subfamily Urotrichinae), but separate from the American true moles, *Scapanus* and *Scalopus*. Conversely, and based largely on tooth morphology, Van Valen (1967) classified the 4 semifossorial genera into 2 distinct, but closely related tribes, Scaptonychini (*Scaptonyx*) and Urotrichini (*Urotrichus*, *Dymecodon*, *Neurotrichus*, plus the fossorial genera *Parascalops* and *Scapanulus*) within the 5-tribe subfamily Talpinae. With slight modifications (Urotrichini sans *Parascalops* and *Scapanulus*), this classification scheme has been accepted by several more-recent authorities (Hutchison 1976; McKenna and Bell 1997; but see

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Table 1.—Examined specimens of 2 species of shrew moles, *Neurotrichus gibbsii* and *Scaptonyx fusicaudus*.

Specimen no.	Species	Sex	Date	Measurements[a]				
				M	HB	Tail	Foot	TR
SIK0425	*N. gibbsii*	♀	24 June 2001	9.00	70.5	35.0	12.0	49.65
SIK0426	*N. gibbsii*	♂	24 June 2001	10.00	66.0	35.0	12.5	53.03
SIK0427	*N. gibbsii*	♂	24 June 2001	—		—	—	
SIK0610	*S. fusicaudus*	♂	31 October 2002	10.40	83.0	32.0	15.0	38.55
SIK0612	*S. fusicaudus*	♂	31 October 2002	10.80	85.0	34.0	13.0	40.00
SIK0613	*S. fusicaudus*	♂	1 November 2002	11.20	81.0	32.0	13.5	39.51
SIK0615	*S. fusicaudus*	♂	1 November 2002	12.40	86.5	32.0	13.5	36.99
SIK0620	*S. fusicaudus*	♂	2 November 2002	9.80	83.0	34.0	13.5	40.96

[a] M, mass (g); HB, head and body length (mm); Tail, tail length (mm); Foot, hind-foot length (mm); TR, ratio of tail length to body length (%).

Hutterer 2005). Myologic and osteologic examinations of the Talpidae moreover considered members of these 2 tribes to be monophyletic (Campbell 1939; Whidden 2000), with the latter author considering *Scaptonyx* and *Neurotrichus* to be closely related sister taxa. Conversely, both the matrix representation with parsimony supertree analyses of Grenyer and Purvis (2003) and the combined genic, cytogenetic, and morphologic data set of Yates and Moore (1990) suggested that the North American and Japanese shrew moles (Urotrichini) form a natural assemblage with the tribes Scalopini (strictly fossorial North American moles) and Condylurini (star-nosed moles) to the exclusion of the Scaptonychini. Both authors closely aligned *Scaptonyx* with the tribe Talpini (strictly fossorial Eurasian moles), a view shared by Ziegler (1971), Hutchison (1976), Moore (1986), and Sánchez-Villagra et al. (2006). Recent molecular (Shinohara et al. 2004) and cranial morphologic (Motokawa 2004) studies similarly failed to support the monophyly of these semifossorial taxa. In fact, Motokawa (2004) and Sánchez-Villagra et al. (2006) suggested that the Japanese, Chinese, and North American semifossorial genera each originated independently. This interpretation is in line with Hutterer's (2005) placement of each group into its own separate tribe within the subfamily Talpinae.

To date, no studies have employed chromosomal characteristics to clarify the phylogenetic relationships among the 4 semifossorial genera. The differential chromosomal banding patterns of the Japanese shrew moles have been well characterized (Hamada and Yosida 1980; Harada et al. 2001; Kawada and Obara 1999); however, comparable published data for the other semifossorial genera are unavailable. Interestingly, although the karyotype of *Scaptonyx* has not been established, that determined from a single American shrew mole (*N. gibbsii*) indicated that the diploid chromosome number of this species (2n = 38—Brown and Waterbury 1971) differs from that of the Japanese shrew moles (2n = 34—Hamada and Yosida 1980). Citing unpublished G-band pattern data, Yates and Moore (1990) further noted *Neurotrichus* differs from Japanese shrew moles (and North American scalopine moles) "by one reciprocal translocation, one pericentric inversion, and by two fission events." Although no indicative G-banding figure was presented, this assertion suggests that substantial karyotypic differentiation has occurred between these 2 groups. Unfortunately, without comparable cytological data from *Scaptonyx*, the timing and evolution of these modifications are difficult to evaluate. To this end, we characterized the chromosomal constitution and differential banding patterns of both the American shrew mole and Chinese long-tailed mole, and compared them to those obtained from the 2 Japanese shrew mole genera (Kawada and Obara 1999).

Materials and Methods

Five live *S. fusicaudus* Milne-Edwards, 1872, were collected in pitfall traps at an elevation of approximately 3,900 m on Laojun Mountain, Lijiang District, Yunnan Province, China. Three *N. gibbsii* Baird, 1858, were captured in similar manner near Blaine, Whatcom County, Washington (approximately 50 m above sea level). Specimen data are presented in Table 1.

Animals were sacrificed in the field and bone marrow cells immediately suspended in a hypotonic solution. Tissue samples were subsequently cultured and fixed at the Kunming Zoological Institute, Chinese Academy of Sciences (*Scaptonyx*), or at the Highland Animal Experimental Station of Nagoya University (*Neurotrichus*). Chromosomal G-bands were obtained with the Giemsa staining, ASG method of Sumner et al. (1971), whereas C-bands were prepared following the BSG method of Sumner (1972). Karyotypes were arranged by size following the standard Japanese shrew mole karyogram of Hamada and Yosida (1980), and the chromosomes categorized as metacentric, submetacentric, subtelocentric, or acrocentric as defined by Levan et al. (1964).

Results

Karyotype of the Chinese long-tailed mole (S. fusicaudus).— The diploid chromosome number (2n) and total number of fundamental autosomal number (FNa) of the Chinese long-tailed mole are 34 and 64, respectively. All autosomal chromosomes are biarmed, with the 1st metacentric chromosome being considerably larger than any other (Fig. 1). Chromosomes 2 through 9 are similar in size, with chromosome 5 carrying an obvious secondary constriction in the proximal short arm (Fig. 1a). The X chromosome is small and metacentric, whereas the minute Y chromosome is dotlike.

G-banded and C-banded karyotypes of *Scaptonyx* are shown in Figs. 1b and 1c, respectively. From their G-banding pattern, homologs were identified and numbered. Relatively large

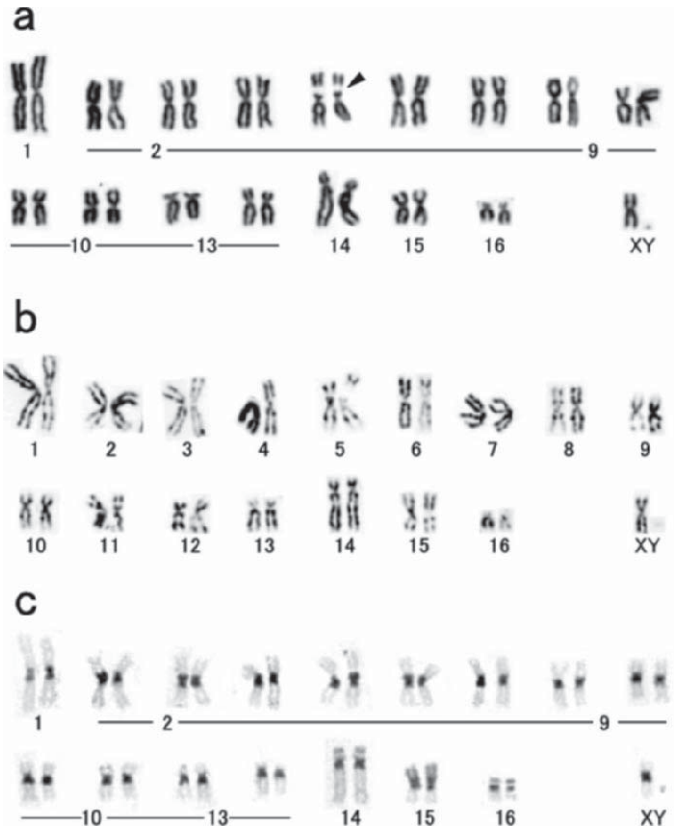

Fig. 1.—Karyogram of a male Chinese long-tailed mole (*Scaptonyx fusicaudus*) illustrating a) conventional, b) G-banding, and c) C-banding patterns. The arrowhead in a) denotes a secondary constriction.

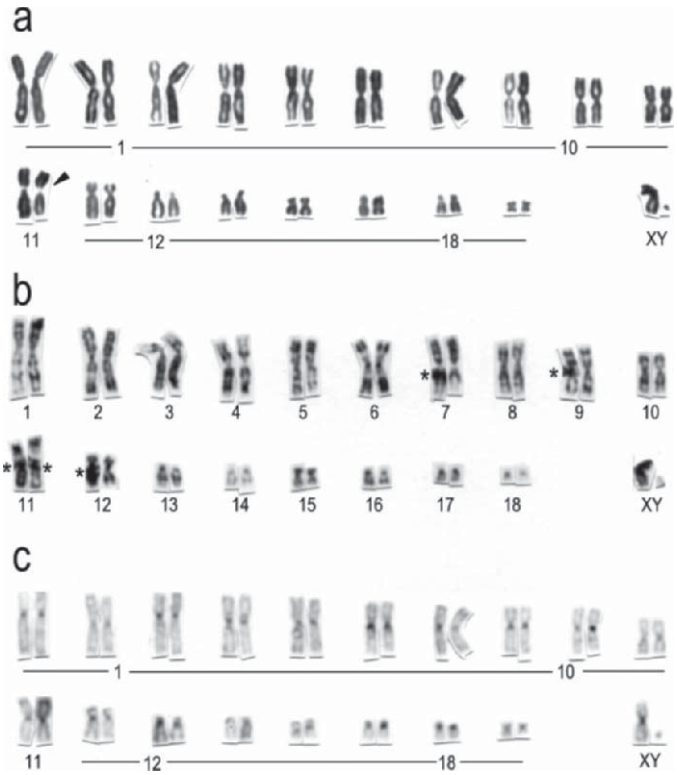

Fig. 2.—Karyogram of a male American shrew mole (*Neurotrichus gibbsii*) illustrating a) conventional, b) G-banding, and c) C-banding patterns. The arrowhead in a) denotes a secondary constriction. Asterisks indicate a crossing of chromosomes.

C-bands distributed along the pericentromeric regions of each chromosome are visible, with the short arm of chromosome 15 (15p) wholly stained as a dark C-block (Fig. 1c). In addition, telomeric regions of the short arms on chromosomes 14 and 16 also are positively stained by the C-banding method. However, these C-bands appear paler than the centromeric C-bands (Fig. 1c).

Karyotype of the American shrew mole (N. gibbsii).—The conventional karyotype of *N. gibbsii* (2n = 38) is composed of 15 biarmed autosomes and 3 small subtelocentric autosomes (Fig. 2a), giving a fundamental autosomal number of 72. The G-banded karyotype identified homologous chromosomes (Fig. 2b). Unlike the Japanese shrew moles, chromosome 1 is only slightly larger than chromosomes 2–11, which are similar in size. All are metacentric chromosomes with little distinction in the Giemsa stained method, except for chromosome 11, which carries a secondary constriction on the proximal short arm (Fig. 2b). Chromosomes 13–18 are small elements of the karyotype, with numbers 13, 14, and 16 being subtelocentric and 15, 17, and 18 being metacentric. As with *Scaptonyx*, the X and Y chromosomes are small-sized metacentric and dot-shaped chromosomes, respectively. Without exception, C-bands are restricted to the centromeric position of each chromosome (Fig. 2c).

Comparisons among the 4 semifossorial talpid genera.—A high degree of similarity in G- and C-banded karyotypes is apparent between the Chinese long-tailed mole (Fig. 1) and the greater and lesser Japanese shrew moles of Japan (Kawada and Obara 1999: figure 2). A composite karyotype of the haploid sets of chromosomes of *Scaptonyx* and *Dymecodon* confirms the G-banding homology between these species (Fig. 3). The primary difference among Japanese and Chinese species is found on chromosome 15, with it being acrocentric in *Dymecodon* (FNa = 62), metacentric in *Scaptonyx* (FNa = 64), and subtelocentric in *Urotrichus* (FNa = 64). Notably, the short arm of this chromosome is C-band positive in the latter 2 species. All other chromosomal elements, including the long

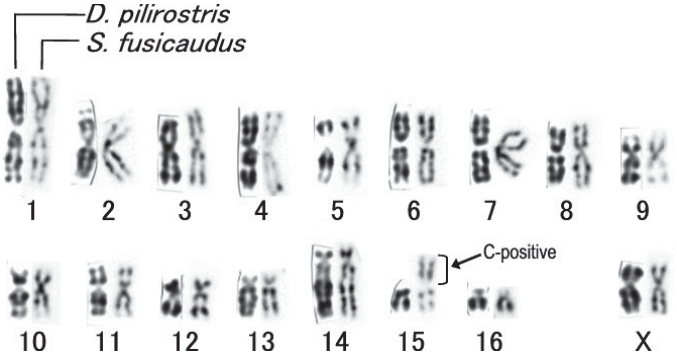

Fig. 3.—Composite G-banded karyotype of the lesser Japanese shrew mole (*Dymecodon pilirostris*; taken from figure 2a of Kawada and Obara [1999]) and the Chinese long-tailed mole (*Scaptonyx fusicaudus*). Note the additional C-positive short arm on chromosome 15 of *Scaptonyx*.

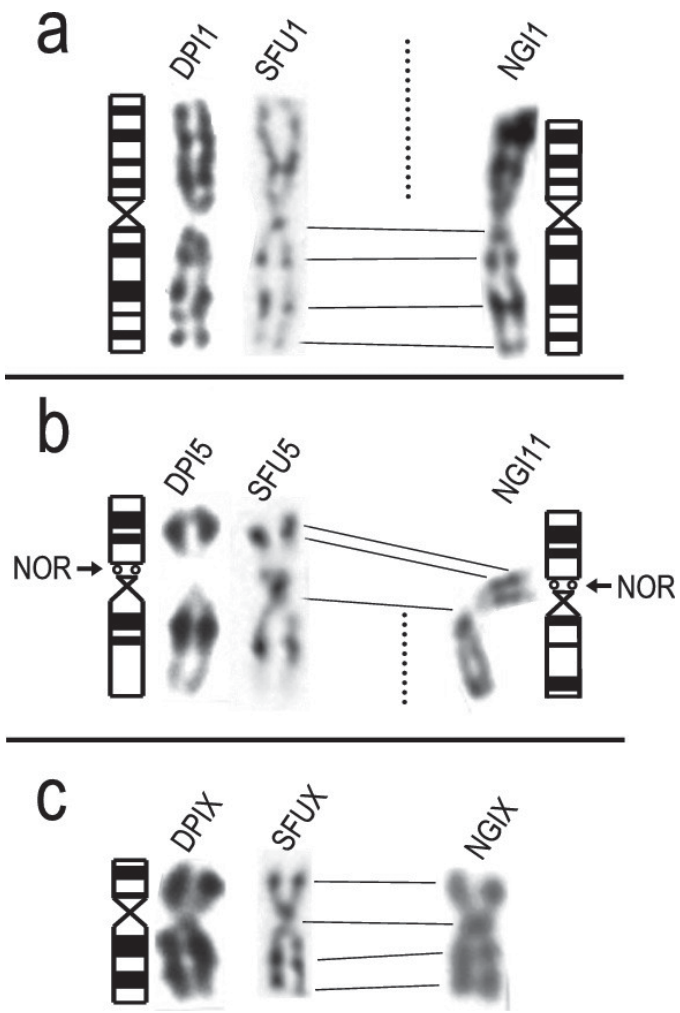

FIG. 4.—G-band comparison of 3 characteristic chromosomes. a) Chromosome 1; b) nucleolus organizer region (NOR)-bearing chromosome; c) X chromosome of *Dymecodon pilirostris* (DPI), *Scaptonyx fusicaudus* (SFU), and *Neurotrichus gibbsii* (NGI). The localization of the nucleolus organizer region (NOR) on the short arm of the secondary constriction carrying chromosomes is indicated.

arm of chromosome 15, are almost indistinguishable in these species, although slight differences are observed in the pericentromeric region of each chromosome, with more distinct positively stained C-banding observed in the Chinese long-tailed mole (compare Fig. 1c with figure 2 of Kawada and Obara [1999]).

All 3 American shrew moles examined possess a higher diploid chromosome number (38) and fundamental autosomal number (72) than the other 3 semifossorial genera (34 and 62–64, respectively). The G-banding pattern of *Neurotrichus* also is very distinctive. For example, the short arm of chromosome 1 in *Urotrichus*, *Dymecodon*, and *Scaptonyx* carries 4 darkly stained bands compared to 3 in *Neurotrichus*, resulting in a noticeably shorter 1st chromosome in the latter taxon (Fig. 4a). The G-banding procedure also revealed a clear terminal band on the long arm of the secondary constriction-bearing chromosome (no. 11) of the American shrew mole, a trait not seen in the corresponding chromosomes (no. 5) of *Scaptonyx* or *Dymecodon* (Fig. 4b). Conversely, perfect homology among species was observed in sex chromosomes (Fig. 4c).

DISCUSSION

Despite the inclusion of all 4 genera of semifossorial moles in the only cladistic analyses of the family Talpidae conducted to date (Motokawa 2004; Sánchez-Villagra et al. 2006; Whidden 2000), their phylogenetic affinities and hence taxonomic classification remain enigmatic. However, because these analyses solely utilized morphological characters, it is possible that at least part of this ambiguity may result from the shared retention of ancestral characters or convergence in 1 or more character states arising from the similar lifestyle and ecological habits of these species. Although both molecular and cytogenetic approaches have the potential to provide clarity to this debate, nucleotide-based analyses have so far failed to illuminate the interrelationships among these 4 genera (Shinohara et al. 2004). Conversely, several lines of karyological evidence provide credible support for a novel clade uniting the Chinese long-tailed mole with the 2 shrew moles of Japan (i.e., sans *Neurotrichus*) and with close phylogenetic affinities with the American Scalopini moles. Furthermore, examination of our data demonstrates that the differentially stained karyotypes of *N. gibbsii* possess numerous uniquely derived traits not found in Scalopini or other shrew moles, in line with the classification of this genus as a distinct monotypic tribe (Hutterer 2005).

Karyotype evolution of shrew moles.—The diploid chromosome number within members of the family Talpidae is remarkably conserved, varying only from 32 to 48 (Kawada et al. 2002b), with most species carrying 34 or 36 chromosomes in their karyotypes (Yates and Moore 1990; Yates and Schmidly 1975). The 34-type is presumed ancestral, because it is found widely throughout the talpid lineage, including the basal Chinese shrewlike moles of the subfamily Uropsilinae (Kawada et al. 2006), the Japanese shrew moles (*Dymecodon* and *Urotrichus*—Hamada and Yosida 1980), and the fossorial European moles (*Talpa*—Gropp 1969) and North American moles (*Condylura* [Meylan 1968], *Parascalops* [Gropp 1969], *Scapanus* [Lynch 1971], and *Scalopus* [Yates and Schmidly 1975]). Thus, *Scaptonyx* (this study) shares the same ancestral diploid number as the Japanese shrew moles, whereas the 38-type *Neurotrichus* (Brown and Waterbury 1971; this study) clearly represents a derived state. Moreover, the G-banding pattern of the Chinese long-tailed mole is remarkably homologous to that *Dymecodon* (Fig. 3), with the most notable exception being the presence of a C-stained short arm on chromosome 15 of *Scaptonyx* (Fig. 3). A similar, albeit smaller band of C-heterochromatin, also is found on the short arm of this chromosome in *Urotrichus* (Kawada and Obara 1999). Conversely, Japanese shrew moles share numerous terminal faint C-bands on several chromosomes (i.e., 1, 2, 13, and 14—Hamada and Yosida 1980; Kawada and Obara 1999). Although similar terminal bands are observed in the short arm of chromosomes 14 and 16 of *Scaptonyx* (Fig. 1c), they are lacking in *Neurotrichus* (Fig. 2c). These findings imply an additional karyological kinship between Chinese and Japanese species,

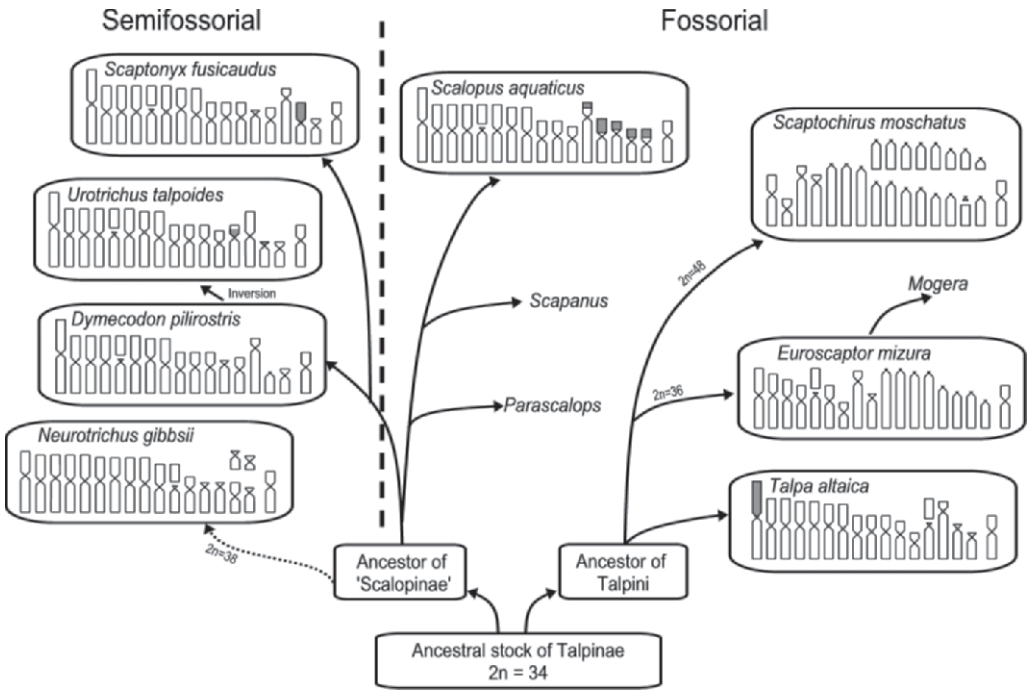

Fig. 5.—Hypothesized karyotype evolution of semifossorial and fossorial moles of the subfamily Talpinae (nomenclature of McKenna and Bell [1997]). The term ''Scalopinae'' refers to Simpson's (1945) subfamily designation for the umbrella group incorporating each of these genera. Sources of schematic karyotypes: *Scaptonyx* and *Neurotrichus* (this study), *Urotrichus* and *Dymecodon* (Kawada and Obara 1999), *Scalopus* (Yates et al. 1976), *Talpa* (Kawada et al. 2002a), *Scaptochirus* (Kawada et al. 2002b), *Euroscaptor* (Kawada et al. 2001). Shaded areas represent putative C-heterochromatic duplication events within each lineage.

and suggests that terminal C-bands accumulated in the latter group after their divergence from *Scaptonyx*.

A pericentric inversion on chromosome 14 clearly delineates shrew moles of the genus *Urotrichus* into 2 distinct geographical (''eastern'' and ''western'') chromosomal races (Harada et al. 2001; Tsuchiya 1988). Kawada and Obara (1999) educed that the direction of this chromosomal change was from subtelocentric (western) to metacentric (eastern), based on the observation that this chromosome also is subtelocentric in the lesser Japanese shrew mole. Our data are in accord with this conclusion, because the corresponding chromosomes of *Scaptonyx* also are medium-sized and subtelocentric, with a G-banding pattern similar to that of *Dymecodon* (Fig. 3). The karyotypes of the Japanese shrew moles are further differentiated by the presence of an unusual region of CMA-band–positive chromatin on chromosome 13 of *Urotrichus* (Kawada and Obara 1999). The observation that the homologous chromosome in all specimens of *Scaptonyx* closely matches that of *Dymecodon* (Fig. 3) suggests that this unusual feature arose in *Urotrichus* after its divergence from the latter group. Unfortunately, the remarkable conservation of the karyotypes among these 3 species (i.e., lack of clear synapomorphic traits) limits strong phylogenetic conclusions. However, because each can easily be derived from a common ancestor, we hypothesize the karyotype evolution of Asian shrew moles as shown in Fig. 5. Thus, the Chinese long-tailed mole does not appear to be an intermediate form between mole and shrew mole (Allen 1938), nor does it appear to be directly basal to Talpini and Urotrichini (Van Valen 1967); it is a ''true'' shrew mole (Campbell 1939; Whidden 2000).

The diploid chromosome number of a female American shrew mole was 1st determined as $2n = 38$ by Brown and Waterbury (1971), in agreement with our data. Usually, the difference in diploid chromosome number among closely related species is caused by Robertsonian translocations and the fundamental autosomal number persists. However, the fundamental autosomal number of the American shrew mole (72) is much higher than that of the other shrew moles (62–64), suggesting that a more complex suite of changes occurred in the chromosomal evolution of *Neurotrichus* than proposed by Yates and Moore (1990). Referring to unpublished data, these authors stated that the G-banded karyotype of *Neurotrichus* differs from that of Japanese shrew moles ''by one reciprocal translocation, one pericentric inversion, and by two fission events.'' Based on this statement, it appears that Yates and Moore (1990) employed the most-parsimonious rearrangements possible to explain the observed differences of diploid chromosome number and fundamental number between these species. However, given that 1 pair of small acrocentric chromosomes is found in *Urotrichus* and 2 pairs in *Dymecodon* (Hamada and Yosida 1980; Kawada and Obara 1999), we should find at least 6 pairs of acrocentric elements with long/short arm homologies in the karyotype of *Neurotrichus* following 2 fission events, yet only 3 small subtelocentric pairs (nos. 13, 14, and 16) are present (Fig. 2). The presence of 3 additional pairs of small metacentric chromosomes (nos. 15,

17, and 18) in *Neurotrichus* underscores the distinctiveness of the karyotype. We also were unable to identify the reciprocal translocation and pericentric inversion events suggested by Yates and Moore (1990). Indeed, similar G-banding patterns between *Neurotrichus* and the Asian genera were generally found only on either the long or short arms of ''homologous'' chromosomes, suggesting that numerous reciprocal translocations occurred since their divergence. For instance, the long arm of the gap-bearing chromosome of the American shrew mole is clearly shorter and markedly differs from that of *Scaptonyx* and *Dymecodon* (Fig. 4b). This chromosome is highly conservative in its banding pattern among members of the subfamily Talpinae (Kawada et al. 2002a, 2002b; Tsuchiya 1988), further emphasizing the uniqueness of the karyotype of *N. gibbsii*. The short arm of chromosome 1 of *Neurotrichus* is also visibly different from that of Asian shrew moles (Fig. 4a). Hence, the chromosomes of Asian shrew moles are more similar to those of North American true moles than to those of the American shrew mole (Fig. 5). It is noteworthy that the G-banding pattern of this large metacentric chromosome in Asian shrew moles closely corresponds to that of North American scalopine moles (Yates et al. 1976); however, its morphology differs significantly from that of Eurasian Talpini moles. In fact, the karyological profiles of North American true moles and Asian shrew moles have more in common with each other than either group does with *Neurotrichus* or the Eurasian true moles (Fig. 5). This close association between Asian shrew moles and North American fossorial moles is generally at odds with nucleotide-based analyses (Shinohara et al. 2003, 2004; but see Cabria et al. 2006). Nonetheless, together with our data, these studies provide additional support that *Neurotrichus* may best be considered as a distinct monotypic group, in accord with Hutterer's (2005) recent taxonomic revision of the Talpidae.

Among higher vertebrates, rates of speciation and chromosomal evolution within genera tend to be accelerated when associated with strong territoriality among individuals, limited vagility, patchy distributions, and the subdivision of populations into small demes (Bush et al. 1977). Although concrete evidence is lacking, anecdotal observations suggest that shrew moles (and moles) possess many of these traits. Unfortunately, nothing is currently known regarding the social organization of *Scaptonyx*, but it is reasonable to assume they may possess similar characteristics. Thus, the high degree of chromosomal conservation among the genera *Urotrichus*, *Dymecodon*, and *Scaptonyx* (and within moles in general) is truly remarkable. Nonetheless, these results are indicative of the preservation of large effective population sizes, and suggest that shrew moles may have originated in continental East Asia. Conversely, theory predicts that chromosomal rearrangements should frequently be fixed in small populations. Examination of fossil data ascribed to *Neurotrichus* from lower Pliocene to middle Pleistocene deposits of Europe suggests that this genus was once quite widespread in distribution (Skoczen 1980). Thus, the numerous autapomorphies apparent within its karyotype, coupled with the small current range of this species, suggests that founder or bottleneck events may have played a prominent role in the early evolutionary history of this genus in North America. Whether substantial intraspecific karyotype evolution occurred following these putative events is unknown, but unlikely because the diploid and fundamental numbers are the same for animals collected from 3 different populations in Oregon (Brown and Waterbury 1971) and Washington (this study; T. Yates, University of New Mexico, pers. comm.). Additional karyotype data from animals spanning the geographical range of this species are clearly required to address this question.

Acknowledgments

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