国立科博専報, (46): 47–56, 2010年3月28日
Mem. Natl. Mus. Nat. Sci., Tokyo, (46): 47–56, March 28, 2010

A Comparative Karyological Study of Taiwanese and Vietnamese *Mogera* (Insectivora, Talpidae) and Classification

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Abstract. Differentially stained karyotypes of three mole species, *Mogera insularis*, *M. kanoana,* and *M. latouchei,* were compared in detail. The diploid numbers of the Taiwanese species, *M. insularis* and *M. kanoana*, and the Vietnamese species, *M. latouchei*, are 2n=32 and 30, respectively, which differ from the Japanese *Mogera* (2n=36). Comparisons of G-banding patterns showed that the differences in diploid number could be explained by two and three Robertsonian rearrangements in the Taiwanese and Vietnamese species, respectively, and that one rearrangement was shared among all three species examined. Additional inversion rearrangements were observed in the Taiwanese species, and two distinct Robertsonian rearrangements were fixed in *M. latouchei*. These karyological data provide important information for the classification of *M. latouchei*, which is currently considered a junior synonym of *M. insularis* in most taxonomic reviews. The taxonomic implications for Taiwanese and Vietnamese *Mogera* are also discussed.
Key words: G-banding, karyotype, *Mogera insularis*, *Mogera kanoana*, *Mogera latouchei*, classification.

Introduction

Moles of the genus *Mogera* are distributed throughout the Japanese islands, Taiwan and the Hainan islands as well as the east coast of continental Eurasia. Those found in Japan are classified into four species, *M. etigo*, *M. imaizumii*, *M. tokudae* and *M. wogura* (Ohdachi *et al.*, 2009), which have been described in recent biological studies (Yokohata, 2005). It is debated whether the mole found from the Korean Peninsula to the far east of Russia can be recognized as an independent species, *M. robusta*, or as same as the Japanese *M. wogura* (Abe, 2005; Hutterer, 2005). In comparison to the Japanese species, the *Mogera* moles occurring in southwestern China, Hainan and Taiwan have not been studied in detail. Swinhoe (1862) published the description of the first species of the Taiwanese mole, *M. insularis*. Subsequently, the southwestern Chinese mole and the Hainan mole were named *M. latouchei* and *M. hainana*, respectively (Thomas, 1907, 1910). These species, however, have been treated as junior synonyms of *M. insularis* in most taxonomic reviews (Abe, 1995; Hutterer, 2005). The taxonomic problems in *M. insularis*

have not yet been resolved, and another species, *M. kanoana*, was recently described from eastern Taiwan, including the mountainous regions (Kawada *et al.*, 2007; also see Yasuda & Kawada, 2007). The authors of the same studies noted that the continental *M. latouchei* is morphologically identifiable from *M. insularis*.

Despite the lack of biological information, *M. insularis* was the first species among the Asian talpids to be investigated with respect to its chromosomal features. Tateishi (1938) demonstrated that their chromosome number is 2n=32 from meiotic observations of serial sections of testis. Recently Lin *et al.* (2002) reported the conventional karyotype from one specimen collected from Pintung City, Taiwan, and confirmed Tateishi's observation. According to Lin *et al.* (2002), the karyotype of *M. insularis* was composed of bi-armed chromosomes and was characterized by only three acrocentric pairs. Kawada *et al.* (2007) also examined the G-banded karyotypes of *M. insularis* and *M. kanoana*, and showed that the chromosome number and G-banding patterns were the same as those of *M. insularis*. In addition, all Japanese *Mogera* species exhibit a diploid number of 2n=36 (Tsuchiya, 1988; Kawada *et al.,* 2001). Therefore, it is important to compare the banded karyotypes between the 32 and 36 chromosome groups. The karyotype of the Chinese *M. latouchei* has not yet been examined, although the species has been recently reported from northern Vietnam (Can *et al.*, 2008; Kawada *et al.*, 2009). We applied banding methods to the chromosomes of Taiwanese and Vietnamese *Mogera* and compared them with the Japanese species to gain insight into the chromosomal rearrangements that have taken place among them.

Materials and methods

A total of eight specimens are used for this study. They are four specimens of *M. insularis* from Hanpao, Chiayi Province and Pintung City, Pintung Province of Taiwan, three specimens of *M. kanoana* from Tatachia, Nantou Province and Manchou, Kenting Province of Taiwan and one specimen of *M. latouchei* from Sapa, Lao Cai Province of Vietnam. Specific identification was done according to previous reports (Kawada *et al.*, 2007; Kawada *et al.*, 2009). Specimens of *M. insularis* and *M. kanoana* were deposited in the Department of Zoology of National Museum of Nature and Science, Tokyo, Japan (NSMT-M), and *M. latouchei* specimens were deposited in the Vietnamese Academy of Science and Technology, Hanoi, Vietnam.

The bone marrow cells of the collected animals were cultured and fixed in the field, using standard procedures with a handle centrifugal manipulator. Tissue samples from skins were brought to the laboratory and cultured. Fixed chromosomes were subjected to differential staining. G-banding and C-banding were done according to the ASG method of Sumner *et al.* (1971) and the BSG method of Sumner (1972), respectively. Giemsa-stained chromosomes were categorized as meta-submetacentric (M), subtelocentric (ST), or acrocentric (A) chromosomes based on Levan *et al*. (1963). C-banding was not done for *M. kanoana*. Silver nitrate staining was performed only for *M. insularis*, according to the one-step method of Howell and Black (1980). Karyotypes for *M. insularis* were arranged based on Lin *et al.* (2002). For the comparative G-banding analysis, we used the G-banded karyotype of the Japanese eastern mole, *M. wogura* (Kawada *et al.*, 2001), because the karyotype of this species is considered to be an ancestral form of the Japanese *Mogera*.

Results

Karyological description of Taiwanese moles, M. insularis *and* M. kanoana

The diploid chromosome numbers of both *M. insularis* and *M. kanoana* showed 2n=32 chromosomal complements without any deviation, and no chromosomal difference was observed between these two species. A conventional Giemsa-stained karyotype is shown in Fig. 1a. The karyotype comprised 24 bi-armed and six acrocentric

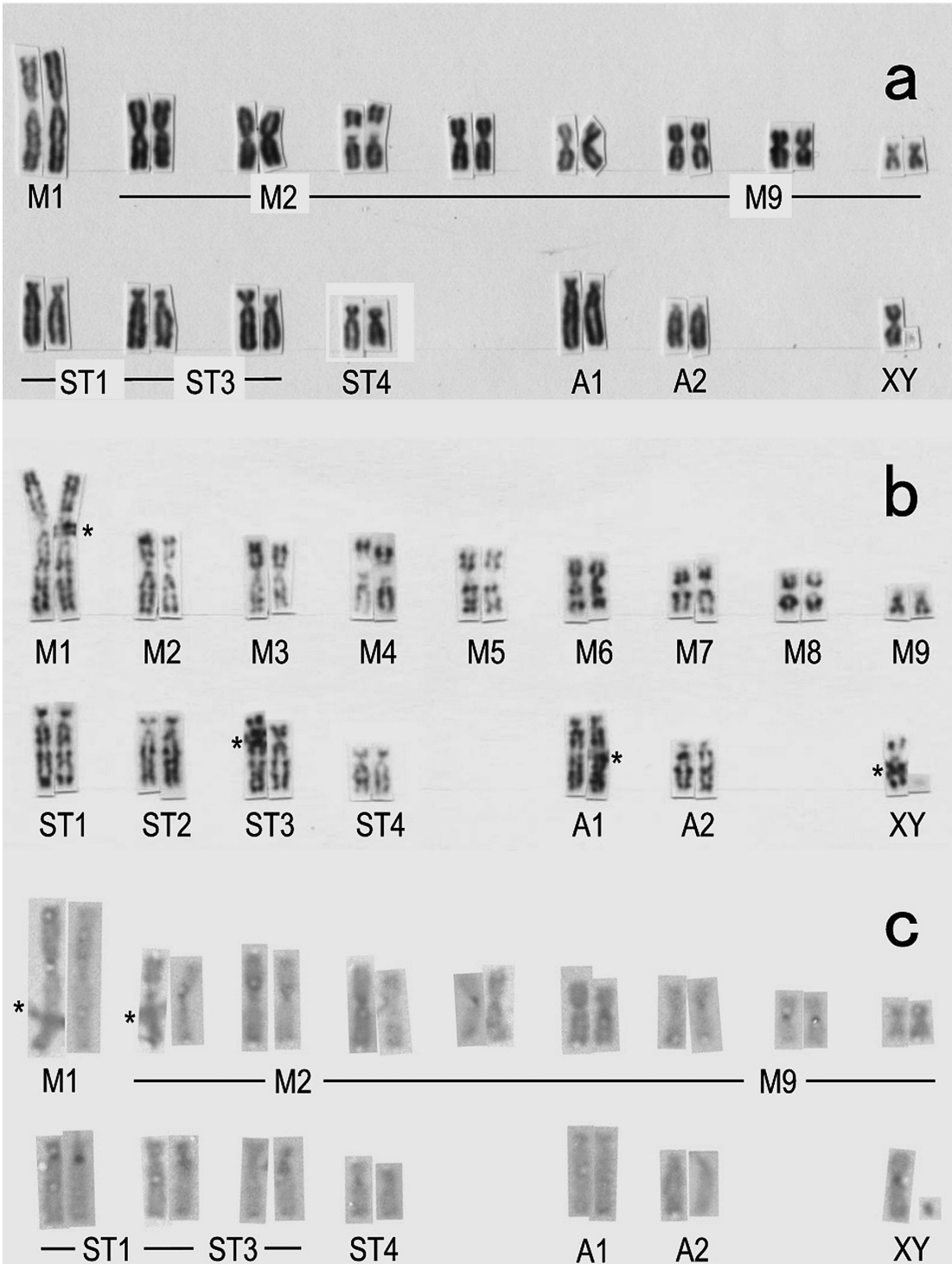

Fig. 1. Conventional (a), G-banded (b) and C-banded (c) karyotypes of male *Mogera insularis* from Taiwan. Asterisks indicate the crossing of chromosomes.

autosomes. Therefore, the fundamental number of autosomes was determined to be NFa＝56. Autosomal chromosome M1 represented a larger M chromosome pair than any other pairs, whereas chromosome M4 had a secondary constriction on the proximal short arm, which appeared as a gap in the Giemsa staining. Numbers M3 to M8 were medium-sized M chromosomes of decreasing size. The ninth was the smallest M-shaped chromosome pair. The karyotype also included four medium-sized ST pairs. The third pair exhibited a rather conspicuous short arm, and the fourth pair was smaller than the others. Of the two A chromosome pairs, A1 was medium sized with a small visible short arm and A2 was small. The X chromosome was a small M chromosome, similar to M4 and M9. The Y chromosome was a dot-shaped, minute chromosome.

The G- and C-banded karyotypes are shown in Figs. 1b and 1c. Each chromosome pair was distinguished based on the particular arrangement of the G-bands and was numbered. The C-bands were localized at the centromeric position of every chromosome, but were very weak.

Karyological description of M. latouchei

The female *M. latouchei* showed a diploid chromosome number of 2 n＝30. A conventional Giemsa-stained karyotype is shown in Fig. 2a. The karyotype comprised 24 bi-armed and four acrocentric autosomes. Thus, the fundamental number of autosomes was NFa＝52. Autosomal numbers M1 to M3 represented large M chromosome pairs, with M1 being the largest and M2 being nearly subtelocentric. M5 was a medium-sized metacentric pair with secondary constriction on the proximal short arm, which appeared as a gap in the Giemsa staining. The fourth to tenth autosomes (M4–M10) were metacentrics of decreasing size, and the twelfth was clearly the smallest metacentric pair. Only one subtelocentric chromosome pair (ST1) and two acrocentric pairs were rather large. The X chromosome was assumed to be one of the small metacentric pairs. Since only a female was examined, the shape of the Y chromosome was not determined.

The G-banded and C-banded karyotypes of *M. latouchei* are shown in Figs. 2b and 2c. The G-banding pattern enabled us to identify each homolog of the autosomal pairs and the X chromosome, which was identified by using the homologous G-banding pattern of the other talpid species (see below). Darkly stained C-bands were localized at the centromeric positions of all chromosomes. Chromosome M1 as well as some small metacentric pairs exhibited rather large C-bands, although chromosome numbers were not determined. The acrocentric pairs A1 and A2 showed typical C-bands on the terminal centromeres.

Comparative G-banding analysis among three species.

The G-banding patterns of two Taiwanese *Mogera*, *M. insularis* and *M. kanoana*, were completely identical at the microscopic level. The G-banded karyotypes of *M. kanoana* and *M. latouchei* were compared with the Japanese congeneric species *M. wogura* (2 n＝36, NFa＝52). Composite G-band karyotypes of three species are shown in Fig. 3. Medium to small metacentric chromosomes, including the X chromosome, of *M. wogura* were shared among the Taiwanese and Vietnamese *Mogera*. In addition, a large subtelocentric pair exhibited the same banding pattern in all three species. G-band incompatibility was observed in the acrocentric series of *M. wogura* (nos. 10 to 17).

The comparison of the G-band karyotypes of *M. kanoana* and *M. wogura* (Fig. 3a) revealed that the Taiwanese M1 was homologous with the G-band pattern of chromosomes 12 and 16 of *M. wogura*. Additionally, the metacentric M2 coincided with 15 and 17 of *M. wogura*. These differences are likely a reflection of Robertsonian fusions. The long arms of the two subtelocentric pairs ST1 and ST3 exhibited the same G-band patterns as the distal parts of 11 and 13 of *M. wogura*, respectively, reflecting two pericentric inversions.

The comparison of G-banding karyotypes between *M. latouchei* and *M. wogura* (Fig. 3b) revealed visible interrelationships between the two

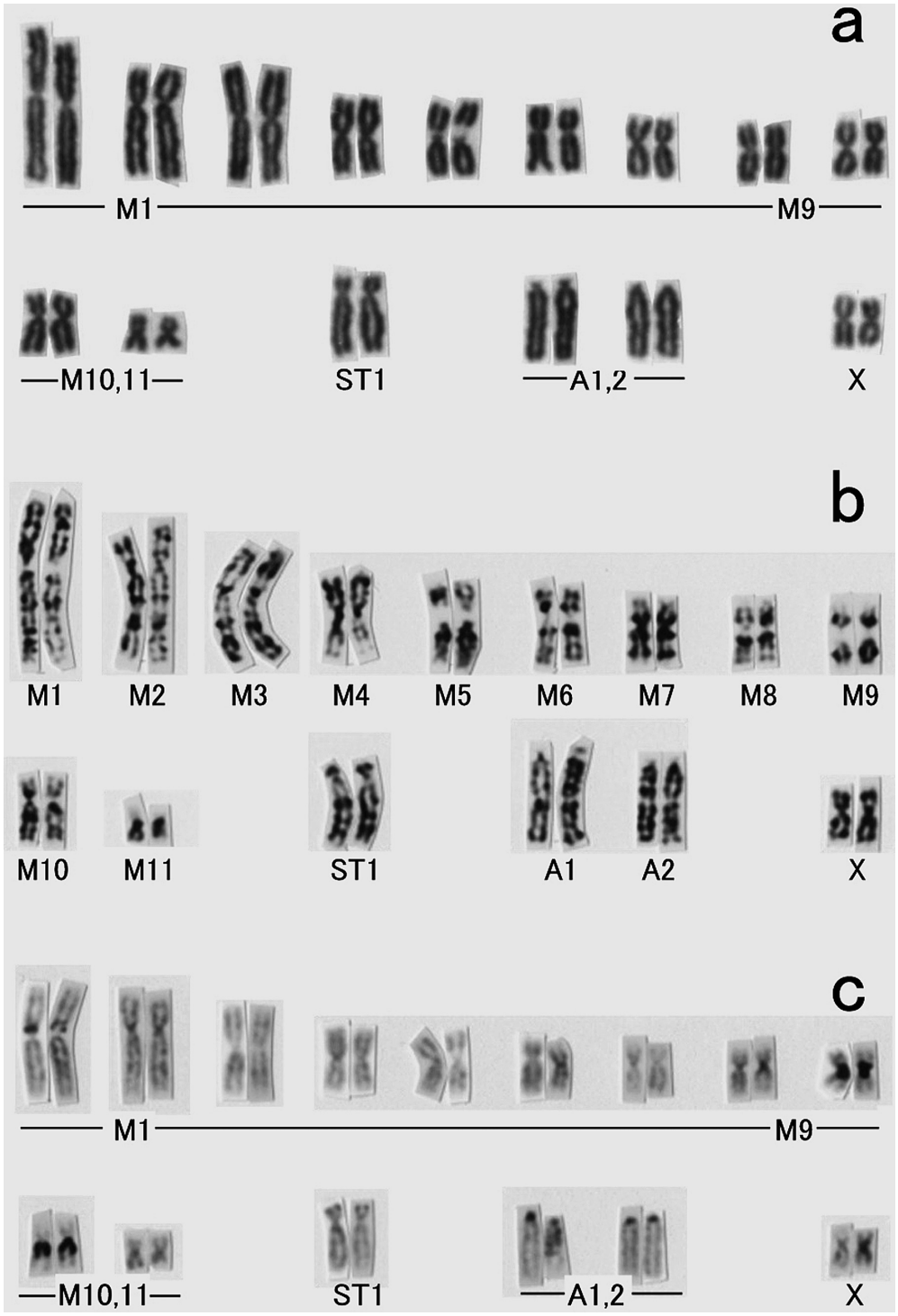

Fig. 2. Conventional (a), G-banded (b) and C-banded (c) karyotypes of female *Mogera latouchei* from Vietnam.

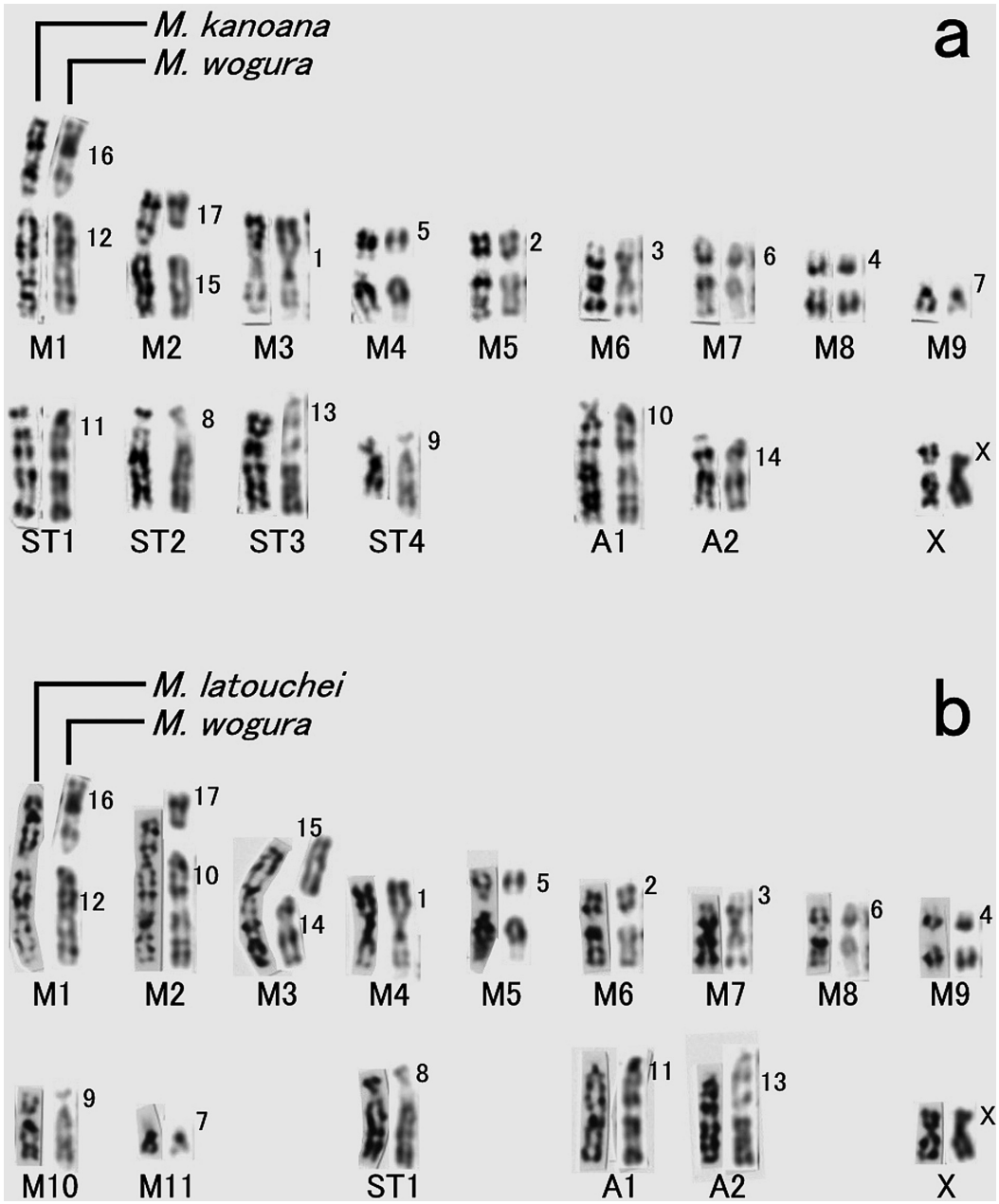

Fig. 3. Composite G-banded karyotypes between *Mogera kanoana* (a) or *M. latouchei* (b) in the left side and *M. wogura* in the right side, shown by arranging the homologous chromosomal elements of *M. wogura* (small letters 1 to 17 and X) from Japan (Kawada *et al.*, 2001).

species. The large metacentric chromosomes M1–M3 coincided with three combinations of acrocentrics in *M. wogura*, *i.e.*, M1 with 12 and 16, M2 with 10 and 17, and M3 with 14 and 15, thus reflecting three Robertsonian rearrangements. The small M10 did not share in the metacentric series of *M. wogura*, and determined to be caused by pericentric inversions of subtelocentric 9 of *M. wogura* based on the G-band homology of the proximal both arms.

The karyotypes of the Taiwanese and Vietnamese *Mogera* were substantially different and shared only one rearrangement, *i.e*., a Robertsonian fusion between chromosomes 12 and 16 of *M. wogura*.

Discussion

Kawada *et al*. (2001) examined only Japanese and Korean species for the comparative karyological study of the genus *Mogera*. All previously identified species, including *M. etigo*, *M. imaizumii*, *M. tokudae,* and *M. wogura* (incl. *M. coreana* or *M. robusta*), exhibited the same diploid number of 2n=36, with distinct fundamental autosomal numbers of NFa=52 to 60. These karyological distinctions were explained by several pericentric inversions fixed in each species, derived from the ancestral karyotype of *M. wogura*. It is considered that the Japanese *Mogera* have a conservative chromosome number with definite inversions and rearrangements. This was supported by the conventionally stained karyotypes of *M. insularis* reported by Lin *et al.* (2002), as well as the G-banded karyotypes of *M. insularis* and *M. kanoana* reported by Kawada e*t al.* (2007). We compared the G-banded karyotypes of the Taiwanese and Vietnamese species with that of Japanese *Mogera* and showed that the karyological profiles of the three species of *Mogera* varied. In particular, the diploid number exhibited by *M. latouchei* (2n=30) is the lowest of all Talpidae. Although Yates *et al.* (1990) suggested that the karyotype of Talpidae was very conservative, our data contradict this.

The diploid number (2n=32) and karyotype profile of *M. insularis* and *M. kanoana* were identical (Kawada *et al.*, 2007). We found that this karyotype differed from that of *M. wogura* by two Robertsonian rearrangements and two pericentric inversions (Fig. 3a), indicating that Taiwanese moles are closely related in a phylogenetic context. Kawada *et al.* (2007) hypothesized that two Taiwanese species of *Mogera* diversified on Taiwan Island after its separation from the Asian Continent. Our data are in accordance with this suggestion, even though *M. kanoana* is morphologically more similar to *M. latouchei* than to *M. insularis*.

The chromosome number of *M. latouchei* was determined to be 2n=30 and is unique within the family Talpidae. *Mogera latouchei* was first described as a species by Thomas (1907) and Stroganov (1948) followed it. Subsequently, however, it has long been considered as a subspecies of *M. insularis* (Ellerman & Morisson-Scot, 1951; Abe, 1995; Hutterer, 2005). This discrepancy may be a reflection of the scarcity of the specimens for detailed taxonomic study. *Mogera latouchei* is the smallest species of *Mogera*. According to Kawada *et al.* (2007), this species exhibits the distinct characteristic of a large, oval auditory opening. The skull is very weakly constructed, and the rostral region is quite narrow. These characteristics make *M. latouchei* morphologically identifiable from *M. insularis*.

The chromosome number data gained from this study support that *M. latouchei* is a distinct species. It is taxonomically important that two of the three large metacentrics of *M. latouchei* represent unique Robertsonian rearrangements. Furthermore, its diploid number, 2n=30, was not caused by simple chromosomal rearrangements. As shown in Fig. 3b, the largest M chromosome of *M. latouchei* exhibited different arm combinations compared with those of *M. insularis* and *M. kanoana*. This monobrachial homology is likely attributable to the fixation of three respective Robertsonian fusions among the four acrocentrics, nos. 10, 14, 15 and 17. Thus, the diploid numbers of the three species are similar, but the constitutions are highly different (see Baker & Bickham, 1986, for the discussion of monobrachial homology).

We determined the fundamental autosomal number of *M. insularis* and *M. kanoana* as NFa=56, although Lin *et al.* (2002) reported as NFa=54. It seemed that ST1 was identified as an acrocentric pair in the previous research. The Taiwanese species carried a subtelocentric chromosome ST1 formed by the proximal pericentric inversion of the acrocentric chromosome 11 of

M. wogura (Fig. 3a), which is a shared characteristic with *M. imaizumii* and *M. tokudae* of the Japanese lineage by mentioned by Kawada *et al.* (2001). This suggests that the Taiwanese *Mogera* was derived directly from *M. imaizumii*; *i.e*., it has never shared a common ancestor with the continental *Mogera*. Shinohara (2008) argued that inversions near the terminal portions of chromosomes occur relatively frequently in humans (Mefford & Trask, 2002), suggesting that the observed subtelocentric chromosome ST1 shared by some *Mogera* is a homoplastic characteristic. In this context, the following two explanations are possible: 1) the hypothetical ancestral karyotype proposed by Kawada *et al.* (2001) is misidentified, or 2) *M. latouchei* and *M. insularis-kanoana* are derived from different origins. In either case, the karyotype changes from Japanese to Taiwanese and/or Vietnamese *Mogera* show that these species do not share a common lineage. We suggest that some karyotype changes occurred after the separation of Taiwanese and Vietnamese *Mogera*.

Our results also provide insight into the species position of *M. kanoana*. Although *M. kanoana* and *M. insularis* have identical karyotypes, *M. kanoana* is morphologically more similar to *M. latouchei* (Kawada *et al.*, 2007). Therefore, considering both the morphological and molecular phylogenetic data, it is suggested that *M. kanoana* is a distinct species from *M. insularis*. Our karyological data support this conclusion. Thus, taxonomically, at least three species of the mole belonging to the genus *Mogera* occur in Taiwan and from southeast China to Vietnam.

It is important that variable diploid numbers were not seen in Japanese and northeastern Asian species of *Mogera*. Our data suggest two distinct trends in the karyotype evolution of the genus *Mogera* in northeastern and southeastern Asia. The Japanese *Mogera* shared the chromosome number, 2 n=36, and experienced several inversion rearrangements (Kawada *et al.*, 2001). Conversely, the southeastern Asian *Mogera* experienced chromosome rearrangements that caused drastic changes in chromosome number by centric fusions. A similar trend is seen in the genus *Euroscaptor*, the sister genus of *Mogera*. Some species of *Euroscaptor* moles possessed karyotypes related via reciprocal translocations among species (Kawada *et al.*, 2005, 2006). We suggest that these trends in karyotype changes are related by some essential factor that contributes to the type of chromosomal rearrangements. It is probable that a physiological mechanism exists to induce taxon-related chromosomal rearrangements. Empirical data show that distinct types of chromosomal rearrangements are repetitively fixed in certain taxonomic groups, which is known as karyotype orthoselection (White, 1978; King, 1993).

In conclusion, the differences of the karyotypes between the two groups of the genus *Mogera* suggest that they diversified far apart within the genus. In a chromosomal context, these two karyotypic groups can be classified as subgeneric positions. Kishida (1937) previously presented this view in Japanese, identifying the Taiwanese *Mogera* as a new genus “Mogerula,” although it was considered to be a *nomen nudum* because the taxonomic treatment was not suitable (Yasuda & Kawada, 2007). Kishida (1937) reported that Japanese and Taiwanese moles differed in their dental morphology; specifically, the first upper premolar possessed one or two roots, respectively. To solve this taxonomic dilemma, further morphological data of the Taiwanese and Vietnamese *Mogera* should be accumulated.

Acknowledgements

The authors express their gratitude to Mr. Chang Kun-Chieh and Ms. Pan Yu-Chieh for their guidance at the collecting localities. Special thanks are also expressed to Dr. Masatoshi Yasuda for giving information about mysterious generic name ‘Mogerula’. We also thank the staff of the Highland Animal Experimental Station, Nagoya University, where a portion of the experiments were conducted.

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台湾およびベトナム産ニホンモグラ属の比較核型分析と分類

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Nguyen Truong Son·Dang Ngoc Can

台湾とベトナムに分布する3種のニホンモグラ属の種について各種染色体分染法を用いて詳細な分析を行い，核型のデータに基づいて台湾とベトナムのモグラについて分類学的に考察した．台湾産のタカサゴモグラ*M. insularis*とヤマジモグラ*M. kanoana*の染色体数は32で，これまでに報告されている知見を支持した．一方でベトナム産フーチェンモグラ*M. latouchei*の染色体数は30であった．これらの染色体数は日本産同属の全種で知られている36とは異なっている．Gバンドパターンの比較により，台湾産とベトナム産の種でそれぞれ2回と3回のロバートソン型転座とそれぞれ2回と1回の挟動原体逆位により日本産の種から核型が変化しており，それらのうち1回の転座は今回調査した3種に共有されていた．これらの核型の変化は，これまでフーチェンモグラがタカサゴモグラのシノニムとして扱われてきた見解に対して，否定的な知見として重要である．