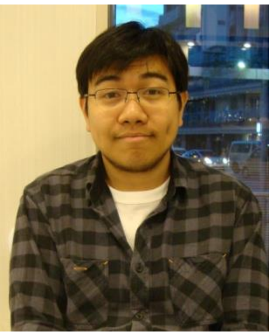

# The Dynamics of Chromosome Evolution in Reptiles
# วิวัฒนาการของโครโมโซมในสัตว์เลื้อยคลาน

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Sauropsida (all existing reptiles and birds) comprises Archosauromorpha (birds, crocodiles, and turtles) and Lepidosauromorpha (tuataras and squamate reptiles). Squamate reptiles have a variable number of chromosomes (2*n* = 30–50), and their karyotypes are basically categorized into two types: the karyotype with few or no dot-shaped microchromosomes; and the other type consisting of macrochromosomes and many microchromosomes (Olmo and Signorino 2005). This karyotypic feature is also observed in birds and turtles, which comprise a small number of macrochromosomes and a lot of indistinguishable microchromosomes (Belterman and De Boer 1984; Olmo and Signorino 2005). On the contrary, the karyotype of crocodiles contains macrochromosomes with only a few large chromosomes, and the absence of dot-shaped microchromosomes. Comparison of the chromosome maps of Chinese soft-shelled turtle (*Pelodiscus sinensis*), Siamese crocodile (*Crocodylus siamensis*), Japanese four-striped rat snake (*Elaphe quadrivirgata*), and butterfly lizard (*Leiolepis reevesii rubritaeniata*) with chicken (*Gallus gallus*) revealed that genetic linkages have been highly conserved between Aves, Testudines, Crocodylia, and Squamata (Matsuda *et al*., 2005; Matsubara *et al*., 2006, 2012; Srikulnath *et al*., 2009a,b; Uno *et al*., 2012) since the Sauropsida diverged from the Synapsida around 320 million years ago (Shedlock and Edwards, 2009).

Comparing karyotypes in the Sauropsida, birds, turtles and crocodiles represent high karyotype conservation, whereas squamate reptiles show great karyotype variability. This appearance probably associated with species richness of Squamata (Olmo 2008). The most common chromosome number in snakes is 2*n* = 36: their chromosomes contain 16 macrochomosomes and 20 microchromosomes, whereas worm lizards show a large variation in chromosome number (2*n* = 30–50; Olmo and Signorino, 2005). The extant lizards (Lacertilia) also exhibit a large variation in both chromosome number (2*n* = 24–46) and chromosome morphology (Olmo and Signorino, 2005). Karyotypes with few or no microchromosomes are found in the lacertid lizards and in geckos, whereas karyotypes containing many microchromosomes are found in the remaining group of squamate reptiles. Such phylogenetic pattern in the presence or absence of microchromosomes suggests that geckos retain the ancestral state of squamate karyotypes, and microchromosomes appeared by the breakage of macrochromosomes that occurred in the lineage of squamate reptiles. However, this chromosomal constitution is not observed in the majority of squamate reptiles; therefore, the alternative explanation is that the microchromosomes disappeared by fusions between macro- and microchromosomes and/or between microchromosomes in the lineage of geckos. Comparison of genetic linkages among squamate reptiles revealed that the linkage groups of squamate reptile macrochromosome segments are highly conserved, and also in some chromosomes of gecko. The remaining of gecko chromosome pairs are composed of chromosome segments homologous to squamate reptile microchromosomes (Matsubara *et al*., 2006, 2012; Srikulnath *et al*., 2009a,b, unpublished data; Uno *et al*., 2012). By contrast, the macro- and microchromosomes of the turtle are actual counterparts of those of chicken, suggesting that the ancestral karyotype of Archosauromorpha, which was probably composed of at least eight pairs of macrochromosomes and many indistinguishable microchromosomes, has been highly conserved more than 250 million years since they diverged from Lepidosauromorpha (Matsuda *et al*. 2005; Shedlock and Edwards 2009; Uno *et al*. 2012).

Interestingly, one different feature between macro- and microchromosomes, which are so-called chromosome size-dependent genomic compartmentalization, is found in chicken and the turtle in term of centromere-specific repetitive sequences. The identification of several types of microchromosome-specific centromeric repetitive sequence in primitive birds, galliform birds, and the turtle (Matzke *et al*. 1990, 1992; Tanaka *et al*. 2000; Yamada *et al*. 2002a, 2002b, 2005) implies that homogenization of the centromeric repetitive sequences did not occur between macro- and microchromosomes in these species. However, no chromosome-specific centromeric repetitive sequences are found in crocodiles (Kawagoshi *et al*. 2008). These findings indicate that the chromosomal size-dependent genomic compartmentalization which is supposedly unique to the Archosauromorpha was probably lost in the crocodilian lineage with the disappearance of microchromosomes, followed by the homogenization of centromeric repetitive sequences between chromosomes. In squamate reptilian lineages, the centromeric repetitive sequences of lacertid lizards (each have only one pair of microchromosomes) were located in the centromeric regions of all chromosomes (Capriglione *et al*. 1989, 1991, 1994, 1998), while those of varanid lizard were located in some macrochromosomes and microchromosomes (Chaiprasertsri *et al*. unpublished data). This suggests that the repetitive sequences have evolved in a concerted manner across macro-and microchromosomes without chromosome size-dependent genomic compartmentalization. Unfortunately, chromosome-specific repetitive sequences have been identified for only a few squamate reptilian lineages, and it is still unknown if this type of repetitive sequences is common in squamate reptiles. More analyses of repetitive sequences are required for other squamate reptiles to obtain a better understanding of the dynamics of chromosome structure associated with karyotype evolution, and to provide insight into the phylogenetic hierarchy of genome evolution in reptiles.

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