19. Parallelism of Karyotype Evolution in Mammals^{*)}

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(Communicated by Sajiro MAKINO, M. J. A., April 12, 1983)

By comparing the karyotypes of the black rat, *Rattus rattus*, with those of the other *Rattus* species, we recognized that the mode of karyotype evolution observed in the former species occurred frequently in parallel fashion with those of the latter species. One good example of parallelism of karyotype evolution is shown in the Ceylonese type black rat with $2n=40$, among which one large metacentric pair derived from the Robertsonian fusion between acrocentric nos. 11 and 12 was included. This karyotype is very similar to the other *Rattus* species, *R. bowersii*, with $2n=40$. Our prediction on the presence of Ceylonese type black rat which had a transient karyotype from the Asian ($2n=42$) to the Oceanian type ($2n=38$) is due to the previous observations of the karyotype in *R. bowersii* (Yosida 1980). We encountered frequently in such parallelism of the karyotype evolution due to the pericentric inversion, Robertsonian fusion and fission in genus *Rattus*. In this paper some examples of the parallelism of the karyotype evolution in genus *Rattus* will be described with a note on a mode of the karyotype evolution in mammals.

1) *Parallelism of the karyotype evolution by the pericentric inversion*: Basic karyotype of the black rat (*R. rattus*) had $2n,42$, characterized by 13 acrocentric pairs (nos. 1 to 13) and 7 small metacentric pairs (nos. 14 to 20) and acrocentric X and Y (Asian type). Chromosome polymorphism due to acrocentrics and subtelocentrics was observed in pair nos. 1, 9 and 13 of this animal. This polymorphism was caused by the pericentric inversion of these three chromosome pairs. As already reported (Yosida 1973, 1980), some other *Rattus* species, such as *R. annandalei*, *R. muelleli*, *R. exulans*, *R. losea* and *R. norvegicus* had $2n,42$, a similar basic karyotype to the Asian type black rat. Pair nos. 1, 9 and 13 in these species, however, were either one of the acrocentric or subtelocentric. *R. annandalei* and *R. muelleli* had only one subtelocentric pair; no. 9 pair is in the former and no. 1 in the latter species. The other two

^{*)} Contribution no. 1479 from the National Institute of Genetics, Japan. Supported by a grant-in-aid for the scientific research from the Ministry of Education, Science and Culture, Japan.

Fig. 1. Parallelism of karyotype evolution in the black rat (*Rattus rattus*) and other *Rattus* species. Polymorphic karyotypes in the Asian type black rat ($2n=42$) are shown in the 1st and 5th lines and the Ceylonese ($2n=40$), Oceanian ($2n=38$) and Mauritius types ($2n=42$) are shown in the 6th, 7th and 8th lines of the left, respectively. Karyotypes of the other *Rattus* species are shown in the right. Bars drawn between the left and right idiograms denote the parallel relation among them. Karyotypes of *R. annandalei*, *R. losea*, *R. exulans*, *R. muelleri* and *R. norvegicus* ($2n=42$) are parallel with any one of the Asian type black rats. Karyotypes of *R. bowersii* ($2n=40$), *R. fuscipes* ($2n=38$) and *R. villosissimus* ($2n=50$) are parallel with Ceylonese, Oceanian and Mauritius type black rats.

pairs in these species were acrocentric. *R. exulans*, and *R. losea* had subtelocentric pair nos. 1 and 9, but no. 13 was an acrocentric. In *R. norvegicus* nos. 1, 9 and 13 were all subtelocentric. These karyotypes were corresponded to any one of the polymorphic karyotypes in the black rat (Fig. 1). The present author (Yosida 1980) once considered that the karyotypes in the *Rattus* species similar to the black rat might have been originated from either one of the polymorphic karyotypes of the Asian type black rat. This consideration, however, must be revised, because Baverstock *et al.* (1983) showed from the huge biochemical data that *R. norvegicus*, *R. exulans*, and *R. losea* could have diverged from the black rat at the early age, before several polymorphic karyotypes of the black rat were differentiated. Thus, the karyotype evolution by the pericentric inversion found in some *Rattus* species seems to have occurred independently from that of the black rat, but with parallel relation among them.

2) *Parallelism of the karyotype evolution by the Robertsonian fusion*: Parallelism of the karyotype evolution in the Ceylonese type black rat and *R. bowellsii* was already described. The Oceanian type black rat with $2n,38$, was characterized by having two large metacentric pairs due to the Robertsonian fusion among four acrocentric pairs (nos. 4, 7, 11 and 12). A similar karyotype to the Oceanian type black rat was found in *R. fuscipes* living in Australia, which had the same chromosome number ($2n=38$) and two large metacentric pairs (Fig. 1) (Yosida 1973). Karyotype evolution by the Robertsonian fusion was observed in *R. leucopus* from New Guinea and *R. conatus* from Australia (Yosida 1973). The former species had $2n=34$, among them four large metacentrics caused by the Robertsonian fusion of 8 acrocentric pairs, and the latter species with $2n=32$ developed by the Robertsonian fusion of 10 acrocentrics. Although in the black rats, the variants with large metacentric pairs more than two pairs are not yet reported so far. Such variants would be expected to find out anywhere in the world by parallelism of karyotype evolution.

3) *Parallelism of karyotype evolution by the Robertsonian fission*: A typical case of the karyotype evolution by the Robertsonian fission has been observed in black rats collected from Mauritius. The latter species was characterized by having two large metacentric pairs similar to the Oceanian type black rat, whereas the chromosome number was 42, being identical with that of the Asian type black rat. Increase of the chromosome number in the Mauritius black rat, however, is due to the Robertsonian fission of two small metacentric pairs, nos. 14 and 18 originally included in the Oceanian type black rat. A parallel karyotype evolution to the Mauritius black rat was found in

R. villosissimus collected in Australia (Baverstock *et al.* 1977; Yosida 1979). Although this species had 50 chromosomes, the basic karyotype is similar to the other *Rattus* species. The karyotype of this species was remarkable by having two large metacentric pairs and 12 small acrocentric pairs (Fig. 1). The former was derived from the Robertsonian fusion, but the latter by the Robertsonian fission of 6 small metacentric pairs (nos. 14 to 19). *R. villosissimus* is independent species from *R. rattus*, and they are distributed in different localities, but the karyotype evolution in these two species seems to have proceeded in parallel fashion.

4) *Mode of the karyotype evolution in mammals*: Parallelism of the karyotype evolution is not only found in the genus *Rattus*, but often in the other rodents and mammalian species. Evolution by inversion was reported in related species in several Rodentia, such as *Peromyscus* (Hsu and Arrighi 1968), *Neotoma* (Baker and Mascarello 1969), *Thomomys* (Patton and Dingman 1970), *Ctenomys* (Reig and Kiblicky 1969) and some others. The parallel karyotype evolution through the Robertsonian fusion was often found in the genus *Mus*. Several subspecies of *Mus minutooides* distributed in Africa had many Robertsonian fusions (Matthey 1966; Jotterand 1972). A similar fashion was found to occur in the tobacco mouse (*Mus poschiavinus*) distributed in Europe (Gropp *et al.* 1970; Capanna *et al.* 1976). The karyotype evolution by the Robertsonian fusion was reported in the other taxon, such as Bovidae (Wurster and Benirschke 1968; Evans *et al.* 1973; Buckland and Evans 1978), Equidae (Ryder *et al.* 1978), Felidae (Hsu *et al.* 1963; Wurster 1969) and Primates (Stock and Hsu 1973; Grouchy *et al.* 1977; Dutrillaux 1979).

Species group related closely has generally a similar karyotype, because they have been originated from a common ancestor. This is referred to the basic karyotype by the present author (Yosida 1980). These species could have developed separately from the common ancestor as an independent species by geographical isolation, gene mutation, selection and several other biological events. The chromosome evolution is suggested to be a big event as mechanism for the separation and the speciation. The karyotype evolution, however, seems not to occur at random in some species group, but in parallel fashion among them. At present, the cause of such parallelism of chromosome evolution has remained unknown, but is considered to be a similarity of the chromosome organization in related species.

As another mode of the karyotype evolution, the present author (Yosida 1983) has presented a possibility of the sequentiality of the chromosome evolution in mammals, namely, one chromosome differ-

entiation gives an effect to induce sequentially the other chromosome differentiation. By such sequentiality and parallelism of the karyotype evolution, mammals would have differentiated to many species since Mesozoic to the present time during about 180 million years.

Acknowledgement. The present author is grateful to Emeritus Professor Sajiro Makino, M. J. A., for his critical reading of this manuscript.

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