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The ZW lampbrush chromosomes of birds: a unique opportunity to look at the molecular cytogenetics of sex chromosomes

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Dedicated to Dr. Susumu Ohno on the occasion of his 70th birthday.

This paper concerns the sex chromosomes of birds, their morphology and their molecular biology, matters that have been the principal focus of a highly successful collaborative research programme which was initiated over 10 years ago involving scientists in Japan, Russia, the USA and England.

Birds offer excellent opportunities for a study of this kind for the special reasons that they have well differentiated and strongly heteromorphic sex chromosomes and, because the female is the heterogametic sex, both these chromosomes (Z and W) can be studied at relatively high resolution in the lampbrush form that they assume during the growth of oocytes in the adult ovary. In no other group of animals is this possible.

The greater part of our research on avian chromosomes in the lampbrush form has been carried out on three species of bird: *Gallus g. domesticus* (chicken), *Coturnix c. japonicus* (Japanese quail) and *Columba livia* (pigeon), although many other species have featured from time to time in comparative aspects of our studies. *G.g. domesticus* and *C.c. japonica* belong to the same order and family (Galliformes: Phasianidae). *C. livia* belongs to the order Columbiformes.

Z and W chromosomes down the microscope

Karyotypes of most modern birds include 5 or 6 pairs of macrochromosomes and between 32 and 36 pairs of microchromosomes. An example of mitotic metaphases from male and female chickens (*Gallus g. domesticus*), with the Z and W chromosomes indicated, are shown in Fig. 1A, B.

It has been shown that vertebrate genomes are mosaics of isochores, which are compositionally homogeneous DNA segments of different GC levels and are correlated with chromosome bands (Bernardi, 1993; Saccone et al., 1997). Birds have relatively small haploid genomes, ranging from 1.2 to 2.5 pg, containing small fractions of repetitive sequences. In a finer scale than that of isochores, the interspersion period of repeated and unique DNA sequences in the avian genome is unusual. Long unique sequences alternate with long clusters of moderately repeated sequences (Epplen et al., 1978; Eden and Hendrick, 1979; Arthur and Straus, 1983). To what extent these peculiarities are reflected in the visible cytological characteristics of bird chromosomes, whether in their metaphase or lampbrush form, remains unclear.

One matter is of special importance and value, and particularly so in view of the ease and success with which it is possible to study the lampbrush chromosomes of birds: bird chromosomes, unlike those of fishes and amphibians, show G and R banding patterns that are as well defined as those of mammalian chromosomes. In almost all respects, therefore, birds present an excellent system for studies in molecular cytogenetics. They have small genomes, well characterized karyotypes, workable lampbrush chromosomes and good female heterogamety allowing both sex chromosomes to be seen in their lampbrush form. Moreover, commercially motivated molecular research on the chicken genome has generated a useful genetic map and made available a wide range of gene sequences that can be used as probes for *in situ* nucleic acid hybridization (ISH).

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