

Chromosomal evolution in the family Phasianidae (Aves)

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The G-banded karyotype of the ring-necked pheasant (*Phasianus colchicus*) shows G-band patterns of the macrochromosomes that are identical with those of the turkey (*Meleagris gallopavo*). The evolutionary relationship between the pheasant and the turkey and some other Galliformes species is discussed.

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According to PETERS (1934) the ring-necked pheasant (*Phasianus colchicus*) belongs to the family Phasianidae, and the turkey (*Meleagris gallopavo*) to the family Meleagrididae. The classification of the two species into different families is based on comparable anatomical and morphological characters being too different to suggest a closer classification. However, results from recent studies of morphological characters (SCHNELL and WOOD 1976) do not suggest that the turkey is substantially taxonomically different from the pheasant or the domestic fowl (*Gallus domesticus*) in the Phasianidae family.

The taxonomy of the Galliformes species has aroused interest from biochemists. All authors agree that the turkey is very similar to species in the Phasianidae family. SIBLEY (1960), studying eggwhite proteins, could not see any real justification for retaining turkeys, grouse and guinea fowl in separate families. SARVELLA et al. (1977) conclude, after studies based on electrophoresis and immunoelectrophoresis of serum albumins, that "there appears little reason to separate the chicken and the turkey into separate families". NOLAN et al. (1975) and PRAGER and WILSON (1976) using microcomplement fixation tests on nine proteins, suggest that the lineage leading to the ring-necked pheasant diverged from that leading to the chicken at least as early as the lineage leading to the turkey.

Unbanded karyotypes of the three species domestic fowl, pheasant and turkey were compared by STENIUS et al. (1963). They observed that "the pheasant and the turkey despite belonging to different families have chromosomal complements of pronounced similarity".

In this study we show that the G-banded macrochromosomes of the pheasant and the turkey are identical. The consequences of this similarity for the evolutionary relationship between the pheasant and the turkey are discussed.

Material and methods

Skin and muscle tissue from about half-brooded foetuses of three male pheasants (*Phasianus colchicus*) were taken for culture in Eagle's Medium supplemented with HEPES to a final concentration of 2×10^{-2} M and with 20 % calf serum. The cells were cultured at 37°C and examined as primary cultures. $1 \mu\text{g/ml}$ colchicine was added 6–8 h before harvesting the cells. After trypsination, the cells were treated for 12–15 min in 0.075 M KCl. The cells were fixed in 3:1 methanol-glacial acetic acid with three changes, dropped on wet slides and air dried. For G-bands, a modification of the technique of WANG and FEDOROFF (1972) was used (RYTTMAN et al. 1979). Alternatively, chromosomes were stained without pretreatment in 2 % Giemsa for 10 min.

Results

We consider the seven largest pairs of chromosomes including the Z-chromosome to be macrochromosomes. The diploid number of microchromosomes is around 66 (Fig. 1).

In Fig. 2 the G-band patterns of the macro- and the nine largest pairs of microchromosomes are

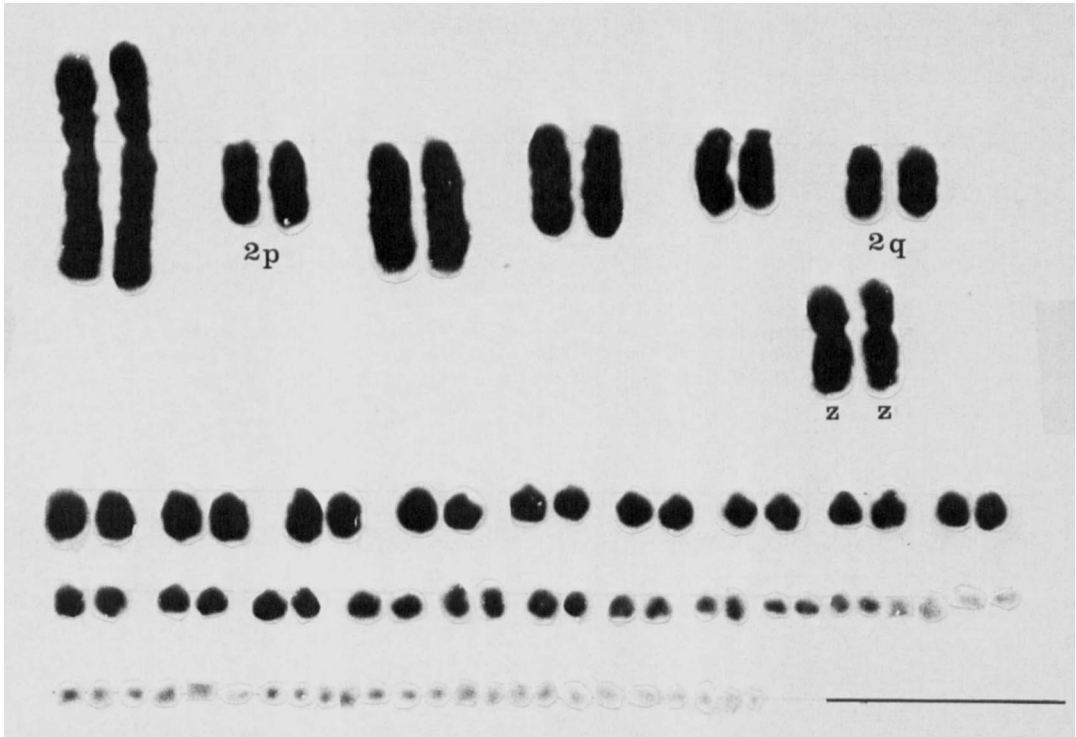


Fig. 1. Giemsa-stained karyotype of ring-necked pheasant (*Phasianus colchicus*) (male) with seven pairs of macrochromosomes including the Z-chromosomes and 33 pairs of microchromosomes. Bar $10\mu\text{m}$.



Fig. 2. G-banded karyotype of ring-necked pheasant (*Phasianus colchicus*) (male) with seven pairs of macrochromosomes including the Z-chromosomes and the nine largest pairs of microchromosomes. Bar $10\mu\text{m}$.

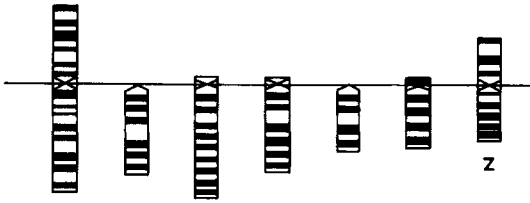


Fig. 3. A schematic drawing of the G-banded macrochromosomes and the Z-chromosome of the ring-necked pheasant (*Phasianus colchicus*).

shown. The G-band patterns of the pheasant's karyotype are very similar to those of the turkey (RYTTMAN and TEGELSTRÖM 1981). A schematic drawing of the G-banded macrochromosomes of the pheasant is shown in Fig. 3.

The nomenclature for the chromosomes of the pheasant has been adapted from CARLENIUS et al. (1981) referring to the chicken chromosomes. We suggest that a centric fission in chromosome no. 2 has resulted in two chromosomes denoted 2p and 2q as in the turkey.

Discussion

STENIUS et al. (1963) found the "almost identical chromosomal constitution quite unexpected" when they compared the chromosomes of the turkey and the pheasant, the turkey and the pheasant belonging to different families. In other animal classes the karyotypes usually are quite separate and easy to distinguish even between species in the same genus.

Since 1963 other examples have been discovered among birds where different families have identical karyotypes. In the order Charadriiformes *Recurvirostra avosetta* (Recurvirostridae) and *Charadrius hiaticula* (Charadriidae) (HAMMAR 1970) and even for different orders, e.g., *Phoenicopterus ruber* (Phoenicopteriformes), *Bugeranus carunculatus* (Gruiformes) and *Sarcoramphus papa* (Falconiformes) (TAKAGI and SASAKI 1974) apparently identical karyotypes have been found.

Several investigators have pointed out the often identical banding pattern of morphologically identical chromosomes in related species. Therefore, it is no surprise that the identical karyotypes of the turkey and the pheasant display the same G-band patterns.

Birds in the same genus often have identical karyotypes. The majority of hybrids between

species in the same genus are known to be fertile. Even species with different karyotypes, e.g., *Anser rossii* and *A. canagicus* have proved to be fertile (SHOFFNER et al. 1979). Therefore, identical karyotypes even with respect to the G-bands do not always give information about the taxonomic relationship of the species or the possibility for interaction between the genomes. Many species in the Phasianidae family have karyotypes identical with that of the ring-necked pheasant. Karyotypes which are very similar to those of the pheasant and the turkey are shown by *Colinus virginianus*, *Callipepla squamata*, *Lophortyx gambeli* and *L. californica* (four North-American quails) (SHOFFNER 1974), The Reeve's pheasant (*Syrnaticus reevesi*) (ITO et al. 1969) and the golden pheasant (*Chrysolophus pictus*) (BENIRSCHKE and HSU 1971), with a centric fission of the second chromosome.

Other karyotyped species in the Galliformes order have karyotypes with biamed chromosomes no. 2, *Crax (Mitu) mitu* (BENIRSCHKE and HSU 1971 and DE BOER and BELTERMAN 1981), *Coturnix (Excalfactoria) chinensis* (KING 1970), *Coturnix coturnix japonica* (e.g., RYTTMAN and TEGELSTRÖM 1981), *Pavo cristatus* (e.g., SASAKI et al. 1968), *Numida meleagris* (e.g., BENIRSCHKE and HSU 1971), *Acryllium vulturinum* (TAKAHASHI and HIRAI 1974) and *Afropavo congensis* (DE BOER and VAN BOCKSTAELE 1981).

Indeed, the second largest chromosome is metacentric in about 80% of all bird species karyotyped. The G-band patterns of this chromosome are also very similar in several bird orders, e.g., Galliformes, Charadriiformes (RYTTMAN et al. 1979), Columbiformes (STOCK et al. 1974) and probably in other orders (TAKAGI and SASAKI 1974, and RYTTMAN and TEGELSTRÖM 1982). We consider, therefore, a metacentric second chromosome to represent the most ancestral morphology of that chromosome in birds. Consequently we propose that a centric fission has occurred in the second chromosome of the pheasant and the turkey.

On the contrary, we believe that the small metacentric chromosomes number six and seven in length in the *Pavo* and *Afropavo* genera discussed by DE BOER and VAN BOCKSTAELE (1981) have been created by Robertsonian translocations. The reasons for this conclusion are that centric fusions are much more common than centric fissions in animal karyotype evolution, that old lineages such as the ratites have only two metacentric chromosomes among their six macrochromosomes (TAKAGI et al. 1972, and DE BOER 1980), that most birds karyotyped have a low number of macrochromo-

somes (TEGELSTRÖM et al. 1983) and that birds with many microchromosomes (>60) have their chromosomes (number seven and smaller in length) mostly telocentric (TEGELSTRÖM and RYTTMAN 1981).

Although the distribution of hetero- and euchromatin discovered in G-bands in the largest chromosomes is very similar, the information in the chromosomes must be very different. The information not only creates different morphology and anatomy but also influences the viability of the hybrids that can be produced between two species.

The hybrids between the pheasant and the turkey are preferentially sterile males (ASMUNDSON and LORENZ 1957), which indicates incompatibility of the W-chromosome between species and other imbalances between the genomes. These disturbances contrast to the identical G-banded chromosomes of *Larus argentatus* and *L. fuscus* (RYTTMAN et al. 1979). In these species the differences between the genetic materials seem to be minimal, as hybrids have proved to be fertile (TINBERGEN 1953).

According to BRODKORB (1964) fossils in the genera *Gallus* and *Phasianus* have been found in the early Pliocene (ca 12 Myr ago), in the genus *Lophortyx* in the middle of Pliocene (6–7 Myr ago) and in the genus *Meleagris* in late Pliocene (ca 3 Myr ago). These palaeontological determinations indicate relationships between these Galliformes species in agreement with chromosomal and biochemical determinations.

Fig. 4 shows our suggestion for the relationships between some of the Galliformes species. The guinea fowls (Numididae) seem to be the most ancestral group (MAINARDI 1963), and these species have a metacentric second chromosome. From that lineage the genera *Gallus* and *Phasianus* have diverged. *Gallus* retains the metacentric second chromosome but in *Phasianus* the second chromosome was split into two (centric fission). From the *Phasianus* lineage other lineages were derived such as *Meleagris* and *Lophortyx*. Therefore, a common ancestor for at least the turkey, pheasants in different genera, and some North-American quails seems the most likely explanation for the centric fission of the second chromosome.

JOHNSGARD (1973) suggests a classification of the order Galliformes. The lineage leading to the turkey and North-American quails diverged from an ancestral lineage earlier than that leading to the family Phasianidae. As some species in the Phasianidae family have a metacentric second chro-

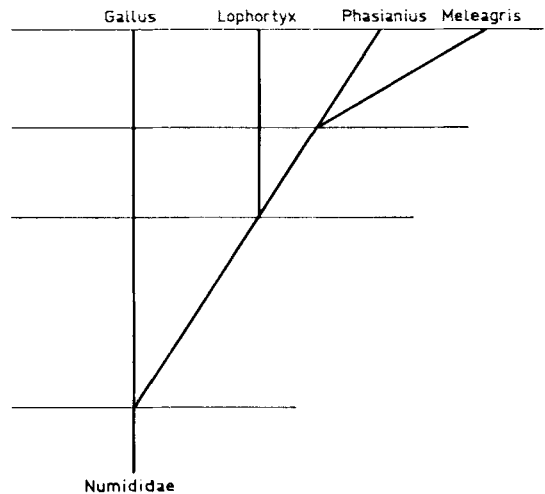


Fig. 4. A diagram showing a proposed relationship between some Galliformes genera including palaeontological, chromosomal and biochemical data.

mosome and other species have their second chromosome split into two, JOHNSGARD's proposal implies two independent centric fissions of the same chromosome: the first when the lineage leading to the turkey and the North-American quails diverged and the second when the Phasianidae family diverged into different genera. This suggestion is more unlikely than the classification proposed by us, which requires only one centric fission (Fig. 4).

However, identical karyotypes do not always reflect a close relationship, and the rate of speciation is different in different environments. WHITE (1978) has proposed that chromosomal rearrangements are necessary in the speciation process. These chromosomal changes could produce changes in regulatory genes preceding the speciation (WILSON et al. 1977). However, we have suggested (RYTTMAN and TEGELSTRÖM 1981) that the speciation process in birds does not normally involve chromosomal rearrangements as a primary step. The speciation in birds probably proceeds by regulatory changes caused by other processes such as recombination. The changes in regulatory genes cause changes in morphology and behaviour display, which in turn create reproductive isolation barriers.

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