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The Compositional Patterns of the Avian Genomes and Their Evolutionary Implications

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Abstract. The compositional distributions of large (main-band) DNA fragments from eight birds belonging to eight different orders (including both paleognathous and neognathous species) are very broad and extremely close to each other. These findings, which are paralleled by the compositional similarity of homologous coding sequences and their codon positions, support the idea that birds are a monophyletic group.

The compositional distribution of third-codon positions of genes from chicken, the only avian species for which a relatively large number of coding sequences is known, is very broad and bimodal, the minor GC-richer peak reaching 100% GC. The very high compositional heterogeneity of avian genomes is accompanied (as in the case of mammalian genomes) by a very high speciation rate compared to cold-blooded vertebrates which are characterized by genomes that are much less heterogeneous. The higher GC levels attained by avian compared to mammalian genomes might be correlated with the higher body temperature (41–43°C) of birds compared to mammals (37°C).

A comparison of GC levels of coding sequences and codon positions from man and chicken revealed very close average GC levels and standard deviations. Homologous coding sequences and codon positions from man and chicken showed a surprisingly high degree of compositional similarity which was, however, higher for GC-poor than for GC-rich sequences. This indicates that GC-poor isochores of warm-blooded vertebrates reflect the composition of the isochores of the genome of the common reptilian ancestor of mammals and birds, which underwent only a small compositional change at the transition from cold- to warm-blooded vertebrates. In contrast, the GC-rich isochores of birds and mammals are the result of large compositional changes at the same evolutionary transition, where were in part different in the two classes of warm-blooded vertebrates.

Key words: Isochores — DNA — Coding sequences — Birds — Mammals — Evolution

Introduction

The genomes of vertebrates are made up of isochores, long DNA segments that are homogeneous in base composition and that can be subdivided into a number of families covering a certain compositional range. This range is very large in warm-blooded vertebrates (e.g., 30–60% in the human genome), whereas it is very narrow in cold-blooded vertebrates. (For a review, see Bernardi 1989, 1993a.)

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Table 1. A classification of birds[a] and the species investigated in the present work

Superorder and order	Family	Species investiaged	
Paleognathi			
Struthioniformes	*Struthionidae*	Ostrich	*Struthio camelus*
Rheiformes	*Rheidae*	Rhea	*Rhea americana*
Neognathi			
Sphenisciformes	*Spheniscidae*	Penguin	*Spheniscus demersus*
Anseriformes	*Anatidae*	Duck	*Cairina moschata*
Galliformes	*Phasianidae*	Chicken	*Gallus gallus*
Charadriiformes	*Laridae*	Herring gull	*Larus argentatus*
Columbiformes	*Columbidae*	Pigeon	*Columba livia*
Passeriformes	*Ploceidae*	Sparrow	*Passer domesticus*

[a] From Perrins and Middelton (1985), except for the introduction of superorders (Sibley and Monroe 1990)

The compositional patterns of large DNA fragments, such as those forming high-molecular-weight DNA preparations, reflect the patterns of isochores and define genome phenotypes (Bernardi and Bernardi 1986) which are distinct not only in cold- and warm-blooded vertebrates but also in birds and mammals (Thiéry et al. 1976; Cortadas et al. 1979) and in some mammalian orders, suborders and infraorders (Salinas et al. 1986; Zerial et al. 1986; Mouchiroud et al. 1987, 1988; Bernardi et al. 1988; Mouchiroud and Gautier 1988, Sabeur et al. 1993). Compositional patterns may also be studied at the level of coding sequences and/or of their different codon positions, because coding sequences are compositionally correlated with the isochores in which the corresponding genes are located (Bernardi et al. 1985; Mouchiroud et al. 1991; D'Onofrio and Bernardi 1992).

In the present work, we have investigated the compositional distributions of large DNA fragments from eight species of birds belonging to eight different orders from both the superorders *Paleognathi* and *Neognathi*. These investigations follow an initial CsCl analysis of DNAs from chicken and herring gull (Thiery et al. 1976) and a detailed investigation of the chicken genome using preparative centrifugation in Cs_2SO_4 density gradients in the presence of two sequence-specific DNA ligands, Ag^+ and BAMD (Cortadas et al. 1979). We have then studied the compositional patterns of coding sequences from the chicken genome, the only avian genome for which a large number of coding sequences are known. Finally, we have compared the compositions of different codon positions for pairs of homologous genes from chicken and man. Both series of sequence analyses follow up initial investigations by Mouchiroud et al. (1987, 1988) and Bernardi et al. (1988).

Materials and Methods

Sources of Animals and Tissues. Red blood cells were used as the starting material for DNA preparations. The species studied were (1) an ostrich and a penguin from a private zoo in Cape Town, South Africa; (2) a rhea from the Vincennes Zoo in Paris; (3) a Muscovy duck and a Leghorn chicken from the animal house of our institute; (4) a herring gull from the Zoology Laboratory of Paris VII University; (5) a pigeon from a pet store; and (6) a sparrow captured in Paris.

DNA Preparations. DNA preparations were made according to Bernardi and Sadron (1964).

DNA Centrifugation and Analysis. Analytical centrifugation in CsCl density gradient was carried out as described previously (Thiery et al. 1976; Bernardi and Bernardi 1990a). Preparative centrifugations of DNA in Cs_2SO_4/BAMD density gradients were done at 20°C and 40,000 rpm for 65 h. BAMD is 3,6-bis (acetato-mercuri-methyl) dioxane (Cortadas et al. 1977, 1979; Macaya et al. 1978). The BAMD/nucleotide molar ratio, r_f, was 0.14, except in the fractionation of rhea DNA (r_f = 0.10).

Sequence Analysis. All coding sequences from chicken and other birds available in GenBank were analyzed for their composition and for that of their three codon positions. Compositional comparisons of coding sequences were investigated as in previous work (Mouchiroud and Bernardi 1993). The sequences used in the present paper derive from release 75 (February 1993).

Results

Table 1 presents the list of the eight avian species studied and a simple classification of the superorders, orders, and families explored. Figure 1 displays the CsCl profiles of the DNAs investigated. Table 2 presents the modal buoyant densities of the DNAs.

In spite of the fact that the orders studied cover the widest possible phylogenetic range, including both paleognathous and neognathous birds, the modal buoyant density range is extremely narrow (1.6997–1.7007 g/cm^3), less than 1 mg/cm^3, with a slightly lower value, 1.6991 g/cm^3, for duck DNA. The second, striking, feature is that all profiles are characterized by relatively large amounts (9–13%) of GC-rich DNA banding at about 1.710 g/cm^3. All profiles show satellite peaks and/or shoulders in the

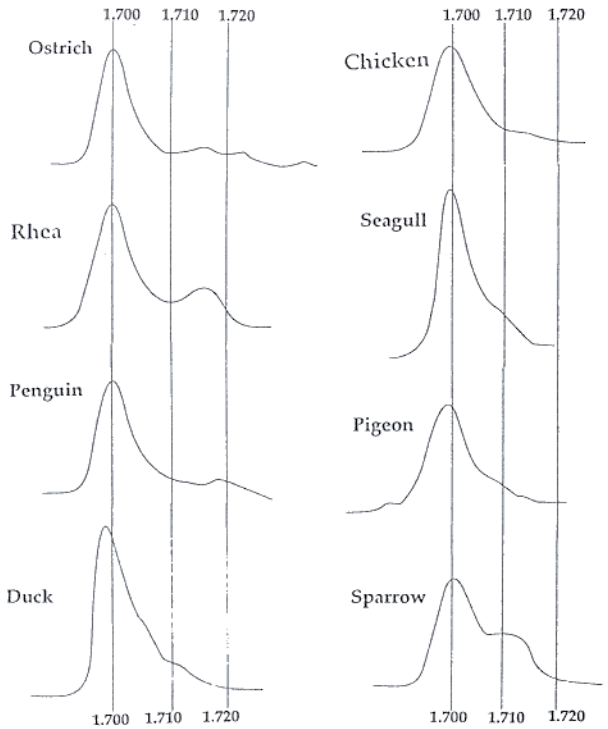

Fig. 1. Analytical CsCl density profiles of unfractionated DNA preparations. The herring gull and sparrow profiles are from Thiery et al. (1976) and G. Macaya (personal comm.), respectively.

Table 2. Modal buoyant DNA densities

DNA source	Total DNA ρ_o	ρ_o	GC-rich DNA Relative amount (%)
Ostrich	1.7001	1.7104	9
Rhea	1.6999	1.7120	9
Penguin	1.7006	1.7096	
		1.7111	10
Duck	1.6991	1.7094	12.5
Chicken	1.6997[a]	1.7094	
		1.7115	
		1.7116	12.4
Seagull	1.6998[b]		
Pigeon	1.7007	.7097	13
Sparrow	1.7002[c]		

[a] Values of 1.7001 and 1.7002 g/cm^3 were reported by Thiery et al. (1976) and by Olofsson and Bernardi (1983), respectively. These values and that in the table are within experimental error
[b] From Thiery et al. (1976). Only analytical CsCl data are available
[c] From G. Macaya (personal comm.). Only analytical CsCl data are available

1.710–1.720 g/cm^3 range, except for duck DNA, which showed, however, two GC-poorer satellite shoulders banding at 1.702 and 1.709 g/cm^3, respectively.

As in the case of mammalian DNAs, satellite peaks are better defined by the CsCl profiles of the DNA fractions obtained after preparative centrifugation in Cs_2SO_4/BAMD (Figs. 2 and 3). Indeed, using this approach, satellite DNAs appear as peaks that are sharper than main-band DNA fractions, and/or do not fit the regular increase in modal buoyant density shown by the latter. If satellite peaks from the GC-rich fractions are disregarded, one can estimate the relative amount of main-band DNA which is equal to, or higher than, 1.710 g/cm^3, in ρ_o. This value was chosen because of the existence in all avian DNAs of a "main-band" component banding very close to 1.710 g/cm^3. This also allowed us an easy comparison with the GC-rich fractions from mammalian DNAs (Sabeur et al. 1993). The amounts of GC-rich DNA components are relatively large (about 10%) in all cases, as summarized in Table 2 and detailed in Table 3.

The compositional distribution of coding sequences and third codon positions of chicken genes (Fig. 4) is roughly bimodal. In the case of third codon positions, the two maxima are centered between 40–60% GC and 75–90% GC. Remarkably, the distribution of the latter, minor peak extends up to 100% GC. This is largely, but not only, due to the contribution of histone genes. The compositional distributions of first and second codon positions expectedly are much narrower than that of third codon positions. Interestingly, the average GC values and standard deviations for coding sequences and third codon positions from chicken are very similar to those from man (Table 4). In fact, if histone genes are neglected, or if homologous genes only are considered, the similarity is extremely high (even for third codon position). In the first of the two latter comparisons, values for chicken and man are closer to each other than values for murids and man.

A plot of GC levels from exons—first, second, and third codon positions (Fig. 5) of homologous genes of chicken and man—showed slopes ranging from 0.99 (for second codon positions) to 0.78 (for third codon positions) and correlation coefficients ranging from 0.96 to 0.73, respectively. A more detailed analysis of third codon positions showed, however, that points below 65% GC exhibit a slope of 0.78 and a correlation coefficient of 0.58, whereas the corresponding values for points above 65% GC are 0.60 and 0.33, respectively (not shown).

Two additional comparisons of third codon positions from homologous genes from chicken and rabbit/artiodactyls and from chicken and murids, respectively (Fig. 6), showed, in the first case, a slope and a correlation coefficient slightly lower than those just reported for chicken *vs* man, and in the second, a lower correlation coefficient, but a higher slope, 1.10.

Finally, a comparison of third codon positions

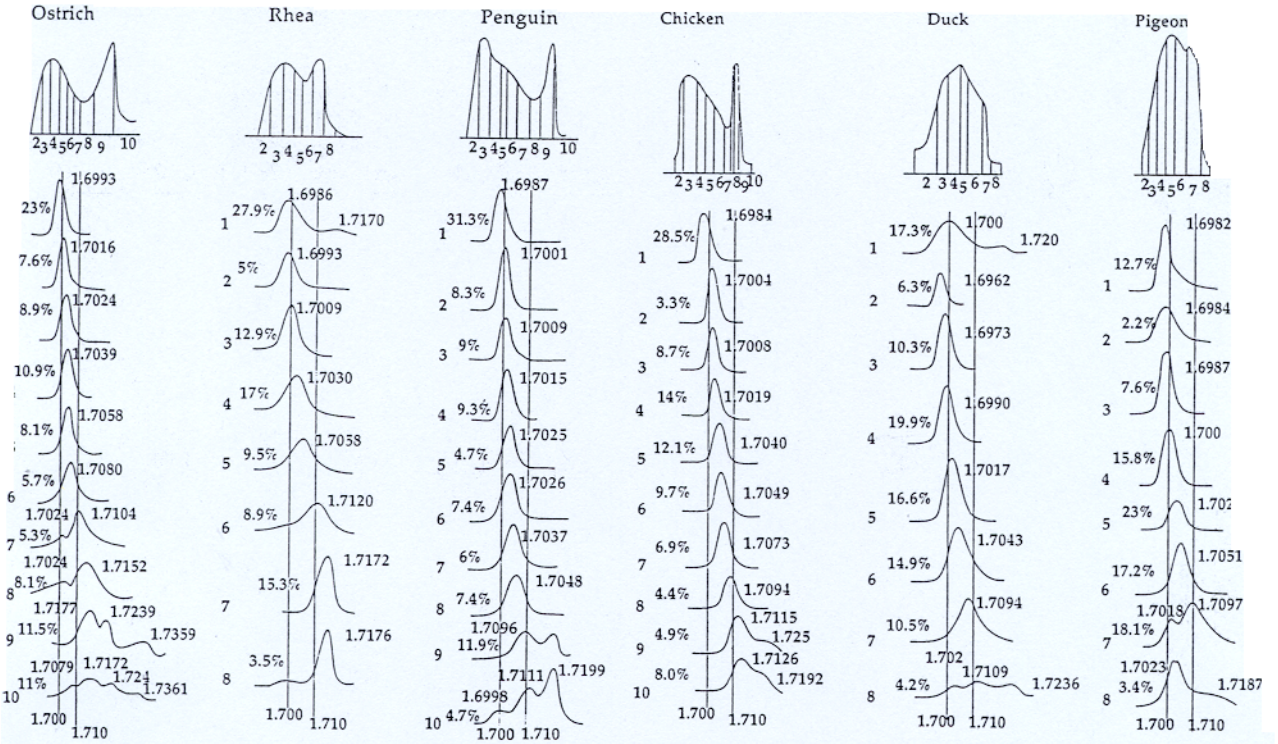

Fig. 2. Fractionation of avian DNAs in preparative Cs_2SO_4/BAMD density gradient. The panels show the analytical CsCl profiles of fractions, the relative amounts of DNA present in them, and the modal buoyant densities of the peaks. Fraction 1 corresponds to pelleted DNA. Loads were 12 A_{260} units per centrifuge tube.

from homologous genes of chicken and other birds (duck, quail, pigeon, goose, turkey, canary) showed a slope of 1.02 and a correlation coefficient of 0.97 (Fig. 7).

Discussion

The Compositional Distribution of Avian DNAs

As already mentioned in the preceding section, the CsCl profiles of all avian DNAs investigated in the present work (Fig. 1) are remarkably similar in modal buoyant density and buoyant density range, the main differences being due to the presence of different satellite DNAs. The extremely narrow range of most modal buoyant densities, <1 mg/cm^3, with one slightly lower value (duck), distinguish avian from mammalian DNAs, whose ρ_o range is about 4 mg/cm^3 for the species explored so far (Arrighi et al. 1970; Sabeur et al. 1993). As in the case of mammalian genomes, a number of satellite DNAs are GC-rich and overlap with GC-rich main-band components.

A more detailed analysis of the compositional patterns of avian DNAs was carried out by fractionating DNA in preparative Cs_2SO_4/BAMD density gradient. In the case of chicken, this analysis (Fig. 2) can be compared with the much more elaborate analysis carried out by Cortadas et al. (1979) using both Cs_2SO_4/Ag^+ and Cs_2SO_4/BAMD fractionations and collecting, in the BAMD case, 33 fractions rather than 10 in the present work. The comparison shows that the DNA having a ρ_o value higher than 1.710 g/cm^3 is estimated at 12.5% in the present work *vs* 10.6% in the previous one. If avian DNAs are analyzed for GC-rich DNA higher than 1.710 g/cm^3 in ρ_o, all of them exhibit significant amounts, 9–13%, of this component, the larger values apparently being the result of overestimations. (See footnotes to Table 3.) In the case of ostrich, part of this component appears to be hidden by a satellite DNA which bands at 1.715–1.717 g/cm^3. The existence in the chicken and in the duck (not shown) genome of genes whose third codon positions reach a 100% GC value suggests that "a minor" DNA component corresponding to these genes extends up to 1.720 g/cm^3, but is hidden by satellite components. The 1.720 g/cm^3 value can be calculated by assuming that the correlation between GC of third codon positions and GC of isochores in avian genomes is the same as that determined in man (Mouchiroud et al., 1991).

The practically identical modal buoyant density and extremely similar compositional distributions of avian main-band DNAs (as well as the data of Fig. 7, see below) support the proposals for a mono-

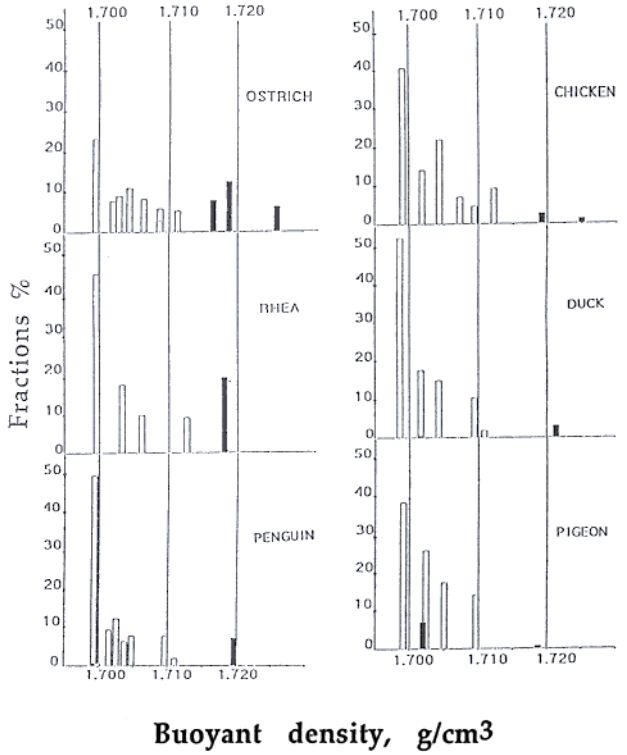

Fig. 3. Compositional distributions of avian DNAs. Diagrams are deduced from Fig. 2. *Black bars* concern satellite DNAs.

phyletic origin of birds (Takagi et al. 1972; Takagi and Sasaki 1974; De Boer 1980; Ansari et al. 1988), in contrast to proposals for a separate origin of ratites, which have been considered a monophyletic assemblage representing the first offshoot in the avian line (Stapel et al. 1984).

A Comparison of Chicken and Human Genes

This comparison may be done in different ways and at different levels of resolution. An overall comparison of all coding sequences or of homologous coding sequences from man and chicken (Table 4) shows a very close similarity, the only difference being a slightly higher GC level and standard deviation in third codon position. This difference disappears, however, if histone genes (which are especially GC-rich in chicken) are neglected, in which case chicken values are closer to the human than to the murid data. The same trend is observed when comparing duck and human data.

A finer level of resolution is provided by comparing the compositional distributions of coding sequences and their codon positions, especially third codon positions. The compositional distribution of third codon positions of chicken genes is bimodal with a separation between the two modes at about 65% GC, with a predominant peak which is GC-poor and a minor GC-rich peak extending up to

Table 3. An analysis of DNA fractions higher than 1.710 g/cm3 in modal buoyant density

Species	Fraction	Relative amount of DNA (%)		ρ_o (g/cm^3)	GC-rich amount (%)
		Fraction	Peaks		
	7	5.3			
			0.3	1.6990 s[a]	
			5.0	1.7104	5.0
	8	8.1	0.1	1.7000 s	
			2.0	1.7110	2.0[b]
			6.0	1.7152 s	
	9	11.5	2.0	1.7110	2.0[b]
			6.5	1.7177 s	
			3.0	1.7239 s	
	10	11.0		1.7079	—[c]
				1.7172	—[c]
				1.724	—[c]
Rhea		27.9			9.0
			27.0	1.6986	
			0.9	1.717 s	
	6	8.9	8.9	1.7120	8.9
	7	15.3	15.3	1.7172 s	
	8	3.5	0.2	1.7001 s	
			3.3	1.7176 s	
					8.9
Penguin	9	11.9			
			8	1.7096	8
			3.9	1.7196 s	
	10	4.7			
			0.7	1.6996 s	
			2	1.7111	2
			2	1.7119 s	
					10[d]
Duck	7	10.5		1.7094	10.5
	8	4.2			
			1	1.7020 s	
			2	1.7109	2
			1	1.7236 s	
					12.5[e]
Chicken	8	4.4		1.7094	4.4
	9	4.5			
			4.0	1.7115	4.0
			0.5	1.7250 s	
	10	8.0			
			5.3	1.7126	4.0
			2.7	1.7192 s	
					12.4[f]
Pigeon	7	18.1			
			5	1.7018 s	
			13	1.7097	13
	8		3.4		
			3	1.7023 s	
			0.4	1.7187 s	
					13[g]

[a] s indicates satellite DNA
[b] Tentative estimates
[c] No estimation was attempted
[d] Slightly overestimated because of the contribution of GC-poorer DNA to the 1.7096 g/cm^3 peak of fraction 9
[e] Overestimated because of the presence of a satellite DNA (evident in the CsCl profile of Fig. 1) in fraction 7
[f] Possibly overestimated on the basis of previous results by Cortadas et al. (1979)
[g] Possibly overestimated because of the likely presence of a satellite DNA indicated by the CsCl profile of Fig. 1

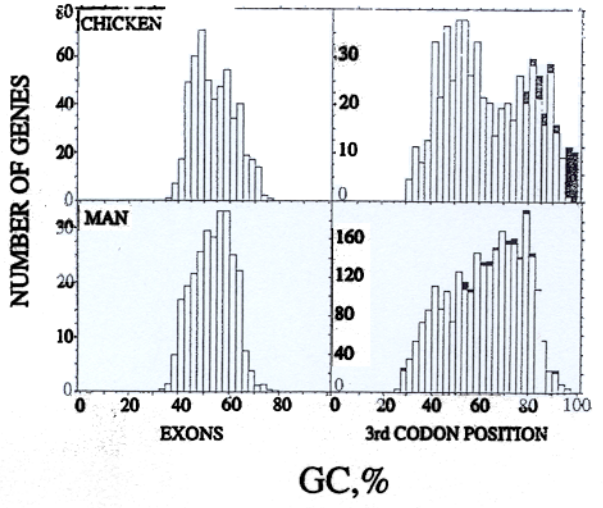

Fig. 4. Compositional distribution of coding sequences—first, second, and third codon positions for chicken and human genes. *Black sections of bars* correspond to histone genes. A 2.5% GC window was used.

100% GC. These findings raise two problems—namely, why does the relative number of genes in the high GC range seem to be smaller in birds than in mammals, and do the higher GC levels attained by third codon positions of avian genes indicate that the chicken genome has a different isochore pattern compared to the mammalian one?

The first question can be approached by comparing GC levels of third codon positions from homologous sequences. (See also next section.) This shows a remarkable compositional similarity between the two sets. Therefore, the only reason the relative amounts of GC-poor and GC-rich third codon positions seem to be so different in the human and chicken genomes is that different genes were investigated. A difference in the compositional patterns of mammals and birds is, however, real, because of the larger amount of 1.710 g/cm^3 DNA in birds and of the higher GC levels attained by third codon positions of chicken (and duck; not shown). Indeed, even if the third codon positions of chicken genes reach 100% GC largely because of histone genes which are lower in GC in man, it is not only because of them. The notion of a GC-richer component, H4 (Bernardi 1989), present in chicken, but not in man, should, therefore, be maintained.

It has been proposed (Bernardi 1993b) that the speciation rate of mammals is higher than that of cold-blooded vertebrates because the GC-rich isochores of the former are heterogeneous, have a more open chromatin structure, and have a higher frequency of repeated sequences. In this connection, it is interesting that the large compositional heterogeneity of the avian genome and the increasing richness in interspersed repeats in GC-richer DNA components (Olofsson and Bernardi 1983ab) are associated with a speciation rate that is even higher than in mammals, as indicated by the existence of about 9,000 avian species (Perrins and Middelton 1985), roughly twice the number of mammalian species. In both cases, the vast majority of such extant species arose over the past 65 Myrs. While chromosomal repatterning is well known in birds (see Christidis 1990), it should be mentioned that the above proposal is in disagreement with the view that "allopatric speciation is clearly the dominant mode in birds" (Sibley and Ahlquist 1990), a view which is also contradicted by the easiness of interspecific hybridization in birds (Grant and Grant 1992).

It has also been proposed that the higher compositional genome heterogeneity of warm- compared to cold-blooded vertebrates is due to a selective advantage having to do with the higher body temperature of the former (Bernardi and Bernardi 1986; Bernardi 1993a). In this connection it is interesting to note that the higher GC-richness attained by the genome of birds correlates with their higher body temperature (41°–43°C; Perrins and Middleton 1985) compared to mammals (37°).

A Comparison of Homologous Genes from Chicken and Man

The comparison of third codon position GC for homologous human and chicken genes is of great interest because it reveals closer values for GC-poor third codon positions than for GC-rich positions. Very interestingly, the separation between the two sets of genes is close to 65% GC, which is the separation between the two peaks in the distribution (Fig. 4). This finding is of interest because it provides a direct support for the concepts of paleogenome and neogenome (Bernardi 1989).

Indeed, a comparison of the genomes as well as of the coding sequences of cold- and warm-blooded vertebrates (Bernardi and Bernardi 1990ab, 1991) indicated that the latter differ from the former in that some isochores (corresponding to about one-third of the genome) and the coding sequences contained in them underwent a GC increase. These compartments of the genome of warm-blooded vertebrates have been called the neogenome to contrast them with the compartments that underwent only a slight change. The results of Fig. 5 indicate that some avian genes that underwent a GC change became richer or poorer in GC than their mammalian homologs, while a certain number of genes apparently underwent a change very similar to that observed in mammals. Among the former, a typical

Table 4. A comparison of compositional properties of genes from man and chicken

Species (& No. of genes)	Coding sequence GC	Coding sequence Std	1st pos. GC	1st pos. Std.	2nd pos. GC	2nd pos. Std.	3rd pos. GC	3rd pos. Std.
All genes								
Chicken (525)	53.8	8.1	55.8	6.7	41.5	7.9	64.1	17.7
(495)[a]							62.4	16.7
Duck (28)	56.4	8.2	57.	5.4	41.5	5.6	70.4	20.4
(20)[a]							61.3	16.5
Man (2772)	53.6	7.7	56.0	7.1	42.2	7.2	62.5	15.5
(2749)[a]							62.4	15.5
Murids (2479)	52.8	6.0	55.0	6.6	41.6	7.0	61.7	11.3
Homologous genes								
Chicken (137)	51.5	7.4	54.6	5.6	39.6	5.9	60.2	16.8
Man (137)	52.3	7.0	55.1	5.1	39.8	5.7	61.7	15.6

[a] Neglecting histone genes

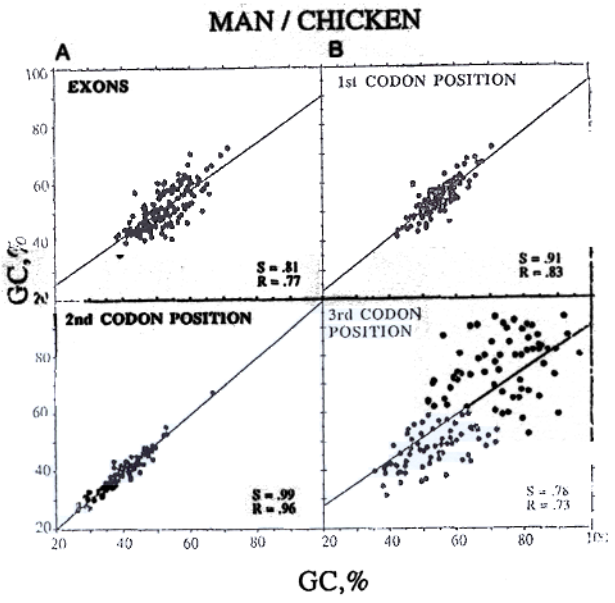

Fig. 5. A Relationships between GC levels of first, second, and third codon positions for pairs of 140 homologous genes from man and chicken. The ordinate corresponds to the human genes and the abscissa to their homologs in chicken. Lines were drawn using the least-squares method. Slopes (S) and correlation coefficients (R) are indicated (B).

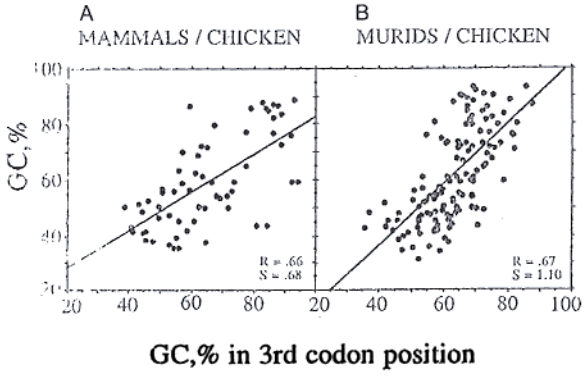

Fig. 6. Relationships between GC levels of third codon positions for pairs of homologous genes from rabbit/artiodactyl and chicken (A) and rat and chicken (B). In the first case, a total of 82 genes were compared—27 from pig, 30 from calf, 17 from rabbit, 4 from sheep, and 4 from goat; genes common to two species (calf and rabbit) were only three. In the second case, a total of 128 genes, 79 from rat and 49 from mouse, were compared.

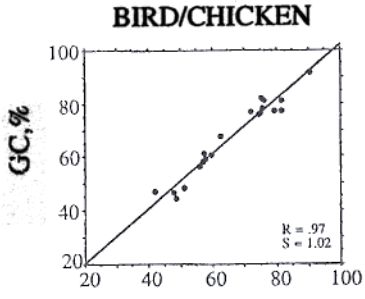

Fig. 7. Relationships between GC levels of third codon positions for pairs of homologous sequences from chicken and other birds (duck, quail, pigeon, goose, turkey, canary).

case is that of genes from the α- and β-globin gene clusters (Bernardi et al. 1985). In chicken, the two clusters are located on different chromosomes and are GC-rich. In man and other mammals, they also are located on different chromosomes, but β-globin genes are GC-poor, whereas α-globin genes are very GC-rich.

In contrast, the genes that underwent a small or no compositional change and that are located in the paleogenome should reflect those of the genome compartments of the common reptilian ancestor of birds and mammals. In other words, the genes located in the paleogenome of birds and mammals are still similar in the composition of their third codon positions, as one would expect for genes from isochores that did not undergo the compositional transition at the times of the appearance of the two

classes of warm-blooded vertebrates (about 220 Myrs ago for mammals and about 150 Myrs ago for birds; Carroll 1988).

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