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Compositional patterns in reptilian genomes

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Abstract

Sauropsids form a complex group of vertebrates including squamates (lizards and snakes), turtles, crocodiles, sphenodon and birds (which are often considered as a separate class). Although avian genomes have been relatively well studied, the genomes of the other groups have remained only sparsely characterized. Moreover, the nuclear sequences available in databanks are still very limited. In the present study, we have analysed the compositional patterns, i.e. the GC (molar fraction of guanine and cytosine in DNA) distributions, of 31 reptilian (particularly snake) genomes by analytical ultracentrifugation of DNAs in CsCl gradients. The profiles were characterized by their modal buoyant density ρ_o, mean buoyant density $\langle \rho \rangle$, asymmetry $\langle \rho \rangle - \rho_o$, and heterogeneity H. The modal buoyant density distribution of reptilian DNAs clearly distinguishes two groups. The snakes fall in the same range of modal densities as most mammals, whereas crocodiles, turtles and lizards show higher values (>1.700 g/cm^3). As far as the more important compositional properties of asymmetry and heterogeneity are concerned, previous studies showed that amphibians and fishes share relatively low values, whereas birds and mammals are characterized by highly heterogeneous and asymmetric patterns (with the exception of Muridae, which have a lower heterogeneity). The present results show that the snake genomes cover a broad range of asymmetry and heterogeneity values, whereas the genomes of crocodiles and turtles cover a narrow range that is intermediate between those of fishes/amphibians and those of mammals/birds.

Keywords: Snake; Crocodile; Turtle; Analytical ultracentrifugation; Base composition; Evolution; Compositional heterogeneity

1. Introduction

Early work from our laboratory showed that the main band of bovine DNA (satellite and minor components are neglected here) is heterogeneous in base composition. Moreover, this heterogeneity is discontinuous, in that it is due to the existence of a small number of families of fairly homogeneous DNA molecules, which cover, however, a wide compositional range (Filipski et al., 1973). Further investigations showed that this heterogeneity was shared by most genomes of mammals and birds (Thiery et al., 1976; Sabeur et al., 1993; Kadi et al., 1993), whereas the genomes of fishes and amphibians were characterized by a much lower degree of heterogeneity (Thiery et al., 1976; Bernardi and Bernardi, 1990), essentially because of the scarcity of GC-rich DNA components which, in addition, do not reach the very high GC levels attained by the genome of warm-blooded vertebrates (Thiery et al., 1976). This pointed to a major discontinuity in the compositional patterns of vertebrate genomes and suggested a compositional transition in the genomes of the ancestors of present-day mammals and birds.

The differences of genome pattern between vertebrates can also be detected in coding sequences (see Bernardi, 2000, for a review). The GC levels of third codon positions, GC_3, in genes of fishes and amphibians cover a relatively narrow range, whereas the range is much larger in birds and mammals, where values can reach 100%. Nevertheless, an exception is observed among mammals: a group of rodents, the murids, show a narrower DNA (Salinas et al., 1986) and GC_3 distribution (Mouchiroud et al., 1988), and their more homogeneous compositional pattern has been recently confirmed using CsCl profiles (Douady et al., 2000). In fact, a good correlation exists between the GC_3 level of a gene and the GC level of the region where the gene is

Abbreviations: A, asymmetry; GC, molar fraction of guanine and cytosine in DNA; *H*, heterogeneity; kb, kilobase pair(s); MW, molecular weight; ρ, buoyant density; ρ_o, modal buoyant density; $\langle \rho \rangle$, mean buoyant density

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located (Bernardi et al., 1985; Clay et al., 1996), indicating that GC_3 level can be used as a marker of isochore families. Finally, when GC_3 levels of orthologous genes from human and *Xenopus* are compared, GC-poor genes share the same average levels, but GC-rich genes are much GC-richer in human than in *Xenopus* (see Bernardi, 2000, for a review).

Under these circumstances, it is of great interest to analyse the genomes of crocodiles, turtles and squamates (lizards and snakes). First, because such an investigation could shed some light on the compositional transition that occurred between fishes/amphibians and mammals/birds if we consider the phylogenetic position of these reptiles (see Zardoya and Meyer, 2001 for the phylogenetic question). Second, because the genome features known so far do not show a consistent pattern, as is the case for the other classes of vertebrates. Indeed, a relatively high compositional homogeneity was observed in the lizard *Iguana iguana* (Thiery et al., 1976) and some other reptiles (Bernardi and Bernardi, 1990), but a turtle, *Testudo graeca* (Thiery et al., 1976) and a snake, *Natrix maura* (Bernardi and Bernardi, 1990), showed a higher degree of heterogeneity. A more detailed investigation on the genome of *T. graeca*, by preparative fractionation in Cs_2SO_4/BAMD density gradients followed by analysis of the fractions in CsCl, confirmed this higher heterogeneity, which was also found in a crocodile, *Crocodylus niloticus* (Aïssani and Bernardi, 1991). Furthermore, although CpG islands could not be found in *T. graeca* and *C. niloticus* (Aïssani and Bernardi, 1991), in contrast with the situation in warm-blooded vertebrates, methylation of reptilian genomes was closer to the lower level of mammals and birds than to the higher level of fishes and amphibians (Jabbari et al., 1997). The analysis of GC_3 values of some coding sequences from a crocodile and a turtle has shown a similarity with their orthologs in chicken (Hughes et al., 1999).

2. Materials and methods

2.1. Taxonomic sampling and DNA extraction

We analysed 31 species of reptiles with a particular emphasis on snakes. The samples, tissues or DNAs, were provided by different laboratories and covered a wide range of species, listed in Table 1. For extraction of DNA from tissues, a protocol modified from Kay et al. (1952) was used. In all cases, the molecular weights of the DNA fragments were controlled by pulsed-field gel electrophoresis (PFGE) on agarose gel with a PFG-low marker. Samples for which the modal molecular weight (computed using Quantity One software) was below 15 kb were excluded from further analysis.

2.2. CsCl profiles

CsCl absorbance profiles of the DNAs were obtained by ultracentrifugation to sedimentation equilibrium using a Beckman Optima XL-A analytical ultracentrifuge. Equilibrium was reached after 24h at a rotor speed of 44,000 rpm. The distances of the DNA distributions from the center of rotation were converted to buoyant densities (ρ) as described in Thiery et al. (1976) using the *Bacillus subtilis* phage 2C as a reference ($\rho_o = 1.742$ g/cm^3). Buoyant densities (given in g/cm^3) were in turn transformed into GC levels by the equation of Schildkraut et al. (1962): $\rho = [(GC \times 0.098)/100] + 1.66$. This relationship is applicable here since the methylation levels of all reptilian genomes analysed so far are below 1.5%, i.e. in the range observed for birds and mammals (Jabbari et al., 1997).

To characterize the DNAs' distribution, different parameters were computed from the CsCl profiles (for details see Thiery et al., 1976; Bernardi and Bernardi, 1990): modal buoyant density, ρ_o, mean buoyant density, $\langle \rho \rangle$, asymmetry, $\langle \rho \rangle - \rho_o$, and heterogeneity, H (defined as the standard deviation of the corresponding GC distribution).

Because of the different experimental set-up of previous investigations, which were done using a Beckman Model E ultracentrifuge, we re-analysed the DNAs of two amphibians (*Rana esculenta*, *Xenopus laevis*), two birds (*Gallus gallus*, *Coturnix coturnix*) and a mammal (*Homo sapiens*), to check the consistency of the values obtained.

2.3. Influence of diffusion

The different parameters used to describe the profiles in CsCl can be influenced by a number of factors, in particular the molecular weight of the DNA sample (Macaya et al., 1976). Heterogeneity (H) was corrected for diffusion by taking into account the modal molecular weights of the samples as follows (cf. Schmid and Hearst, 1972):

$$H^2_{\text{corrected}} = H^2 - \left((25.0082 \times \rho_o)/(0.98^2 \times \text{MW})\right)$$

where $H_{\text{corrected}}$ is the diffusion-corrected heterogeneity in GC%, MW the modal molecular weight in kb and ρ_o the modal buoyant density in g/cm^3. It should be mentioned that the diffusion correction cannot always eliminate all of the molecular weight dependence of the profiles: small-scale ($\leq$1–2 kb) features of the genomes' compositional organization can cause residual dependencies (cf. Macaya et al., 1976; Cuny et al., 1981), at the DNA sequence level, that are not always predictable.

3. Results

3.1. Variability of modal buoyant densities in reptilian profiles

The CsCl profiles obtained for reptiles in this work are shown in Fig. 1. The corresponding species are given in Table 1. The parameter ρ_o provides a good separation of reptilian groups (Table 1 and Fig. 1). Indeed, all the snake DNAs range from 1.6974 g/cm^3 (*Python molurus bivittatus*)

Table 1
Species analysed by analytical ultracentifugation in CsCl gradient and parameters deduced from the profiles

Order/group	Suborder	Superfamily/infraorder	Family	Subfamily/genus	Species	No.	Source	ρ_o (g/cm^3)	$\langle\rho\rangle$ (g/cm^3)	$\langle\rho\rangle - \rho_o$ (mg/cm^3)	$H_{corr.}$ (GC%)	MW (kb)
Squamates	*Lacertilia*	*Gekkota*	*Gekkonidae*		*Gekko gecko tokay*	1	a	1.7032	1.7046	1.4	5.2	16
		Scincomorpha	*Lacertidae*		*Lacerta viridis*	2	b	1.7019	1.7031	1.2	3.5	>60
					Podarcis muralis	3	c	1.7019	1.7025	0.6	3.1	>60
		Diploglossa	*Anguidae*		*Anguis fragilis*	4	c	1.7019	1.7032	1.3	3.2	>60
	Serpentes	*Colubroidea*	*Colubridae*	*Colubrinae*	*Boiga dendrophila*	5	a	1.6997	1.7007	1.0	4.3	>60
					Elaphe obsoleta	6	a	1.6984	1.6993	0.9	3.7	>60
					Gonyosoma oxycephalum	7	a	1.6988	1.7005	1.7	5.1	27
					Lampropeltis triangulum polyzona	8	a	1.6983	1.7011	2.8	6.8	36
					Rhinocheilus lecontei	9	a	1.6996	1.7015	1.9	6.0	21
				Xenodontinae	*Clelia rustica*	10	c	1.6989	1.6995	0.6	2.8	>60
				Boodontinae	*Lamprophis olivaceus*	11	a	1.6995	1.7022	2.7	6.7	45
				Dipsadinae	*Pliocercus euryzona*	12	d	1.7010	1.7014	0.4	3.5	54
					Sibon longifrenis	13	d	1.7005	1.7015	1	4.3	57
					Sibon nebulata	14	d	1.7000	1.7009	0.9	3.9	41
			Elapidae	*Bungarinae*	*Aspidelaps lubricus*	15	a	1.6984	1.7020	3.6	7.6	25
					Walterinnesia aegyptiae	16	c	1.6983	1.6995	1.2	3.5	>60
				Notechinae	*Notechis scutatus*	17	c	1.6980	1.7000	2	4.4	>60
			Viperidae	*Viperinae*	*Bitis gabonica gabonica*	18	a	1.6982	1.7003	2.1	5.5	15
					Vipera ammodytes	19	c	1.6980	1.6991	1.1	3.5	60
				Crotalinae	*Crotalus lepidus*	20	a	1.6985	1.7006	2.1	5.5	29
					Tropidolaemus wagleri	21	a	1.6995	1.7026	3.1	7.3	23
		Henophidia	*Boidae*		*Boa constrictor*	22	a	1.6982	1.6997	1.5	3.5	26
			Pythonidae		*Python molurus bivittatus*	23	a	1.6974	1.6999	2.5	5.3	34
					Python curtus	24	a	1.6983	1.7005	2.2	6.2	18
Turtles	*Cryptodires*		*Emydidae*		*Trachemys scripta elegans*	25	a	1.7006	1.7028	2.2	4.7	>60
					Trachemys scripta elegans	26	c	1.7007	1.7031	2.4	4.9	>60
	Pleurodires		*Pelomedusidae*		*Pelusios subniger*	27	a	1.7002	1.7026	2.4	5.6	5
Crocodiles			*Alligatoridae*		*Alligator mississippiensis*	28	e	1.7017	1.7037	1.9	4.5	>60
			Crocodylidae		*Crocodylus acutus female*	29	d	1.7022	1.7040	1.8	4.3	>60
					Crocodylus acutus male	30	d	1.7026	1.7044	1.8	4.5	60
					Crocodylus niloticus	31	a	1.7021	1.7036	1.5	4.1	>60
Birds			*Phasianidae*		*Coturnix coturnix*	32	f	1.6990	1.7018	2.8	6.4	>60
					Gallus gallus	33	f	1.6996	1.7026	3.0	6.4	25
Mammals			*Hominidae*		*Homo sapiens*	34	f	1.6974	1.6997	2.3	5.6	32
Amphibians			*Ranidae*		*Rana esculenta*	35	b	1.7024	1.7028	0.4	3.1	33
			Pipidae		*Xenopus laevis*	36	f	1.6973	1.6980	0.7	2.9	55

The classification given for reptiles followed the one given in the Reptile EMBL database (http://www.embl-heidelberg.de/~uetz/LivingReptiles.html). Sources: (a) Breeders; (b) Katya Shostak, Kiev; (c) Dusan Kordis, Department of Biochemistry and Molecular Biology, Jozef Stefan Institute, Ljubjana, Slovenia; (d) Heidy Villalobos, Federico Albertazzi, Gabriel Macaya, CIBCM, University of Costa Rica 'Rodrigo Facio', Costa Rica, and Nicolas Carels; (e) Axel Janke, Department of Genetics, Division of Evolutionary Molecular Systematics, University of Lund, Sweden; (f) Nicolas Carels and Giuseppe Bucciarelli, Stazione Zoologica Anton Dohrn, Naples, Italy.

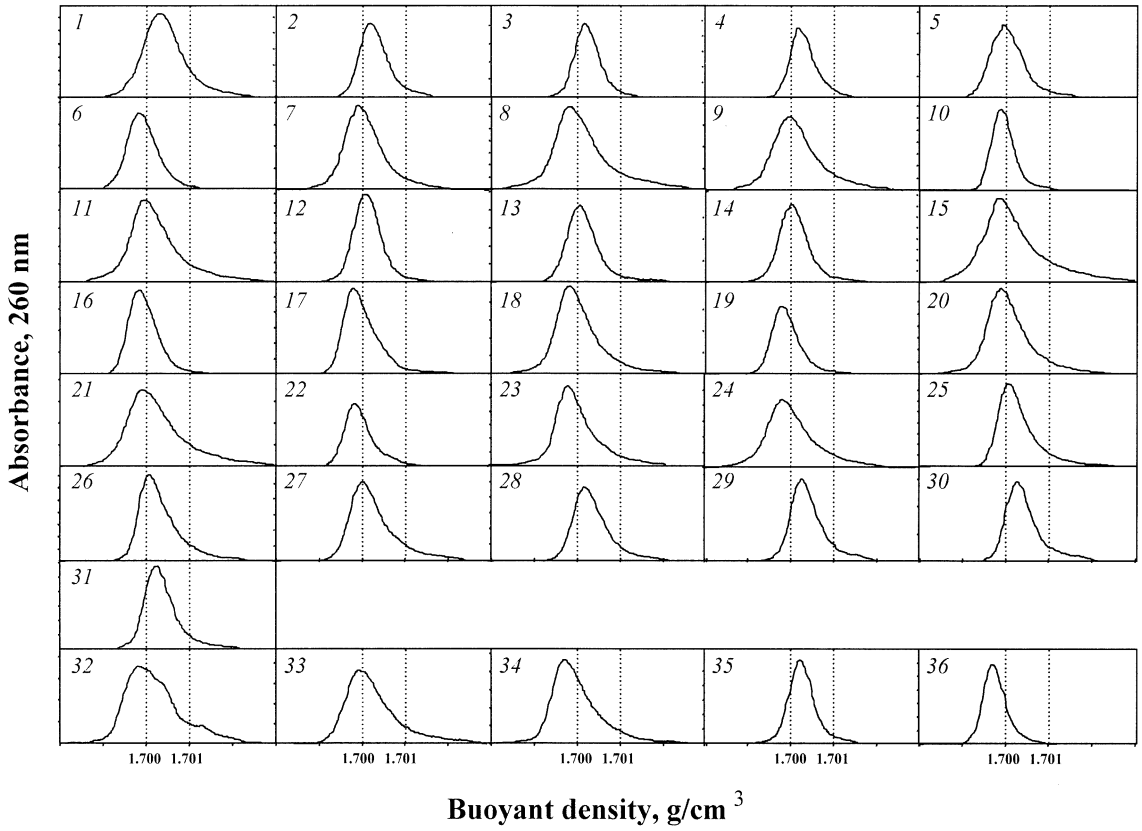

Fig. 1. Reptilian CsCl profiles obtained in this study. Profiles for five other vertebrates are shown in the bottom row. See Table 1 for the numbering of samples.

to 1.7010 g/cm^3 (*Pliocercus euryzona*), with a majority of the species (17/20) below a threshold value of 1.7000 g/cm^3, whereas all crocodilians, turtles and lizards have modal buoyant densities greater than 1.7000 g/cm^3, with a maximum of 1.7032 g/cm^3 (*Gekko gecko*). The tendency of snakes to have lower buoyant densities is in agreement also with early measurements of reptilian GC levels by thermal denaturation (Olmo and Odierna, 1977).

A more detailed analysis confirms that the modal buoyant density can also be valuable to separate species at a lower level of classification, as in the case of rodents (Douady et al., 2000). For example, the three *Dipsadinae* are characterized by the three highest modal buoyant densities (1.7000, 1.7005, 1.7010 g/cm^3) among all *Colubridae* (and even other snakes) analysed here. A CsCl profile previously obtained for another species of *Dipsadinae*, *Tomodon dorsatus*, was in agreement with this tendency since it showed the highest modal density (1.7014 g/cm^3) obtained for snakes (Bernardi and Bernardi, 1990).

Even though the lizards (*Lacertilia*) are phylogenetically closer to snakes (with which they form the clade of squamates) than to other reptiles, the modal buoyant densities obtained for the four new lizard profiles (1.7019–1.7032 g/cm^3) are similar to the crocodilian values (1.7017–1.7026 g/cm^3; Table 1). This slight increase of ρ_o compared to the snakes is in agreement with the previous lizard data (1.7014–1.7047 g/cm^3; Bernardi and Bernardi, 1990). In this scheme, the turtles analysed show intermediate values, although always larger than 1.7000 g/cm^3: 1.7027 g/cm^3 (Thiery et al., 1976), 1.7022 (Bernardi and Bernardi, 1990) and 1.7002–1.7007 (this study).

3.2. Asymmetry and heterogeneity in reptilian genomes

3.2.1. Influence of molecular weight

Asymmetry and heterogeneity are two parameters that are sensitive to the molecular weight of the DNA samples, especially when it is low. Although heterogeneity was corrected for diffusion (see Section 2), a negative relationship with the molecular weight is still detected on the entire data set but the points appear largely dispersed (Fig. 2). This corresponds to the difficulty in precisely predicting how asymmetry and heterogeneity of the GC distribution will vary as a function of the molecular weight (see Section 2.3). The variation observed among the relatively high molecular weights of the DNA samples analysed here is, however, not large enough to explain the sizeable differences in asymmetry and heterogeneity that were observed among the taxa (Fig. 2). In fact, 26 profiles out of the 36 presented here had modal molecular weights above 30 kb (Table 1).

3.2.2. Variability among reptiles

In the species analysed in this study, heterogeneity is well correlated with asymmetry ($R^2 = 0.83$, $P < 0.001$; see

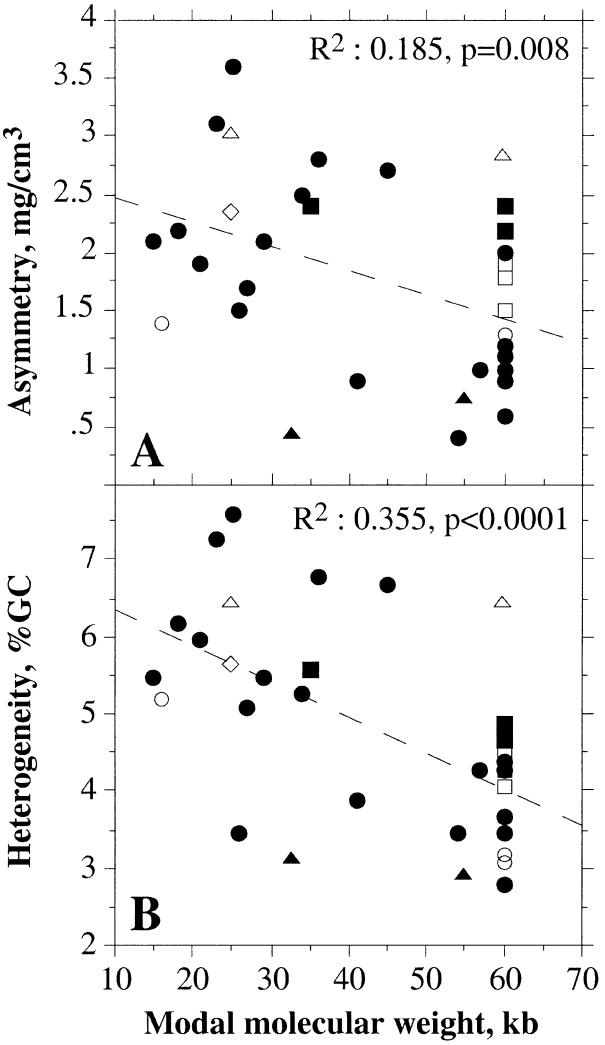

Fig. 2. Relation between modal molecular weight of the DNA fragments and asymmetry (A) or diffusion-corrected heterogeneity (B) computed for the CsCl profiles obtained in this study. Different groups are distinguished: snakes (●), lizards (○), turtles (■), crocodilians (□), amphibians (▲), birds (△) and human (◇).

Table 1). Since asymmetry values are more abundant than heterogeneity in the literature, we will preferentially use asymmetry in the following discussion. All the reptilian genomes studied here show a positive asymmetry, and the two groups discriminated by the modal buoyant densities show different patterns (Fig. 3). On the one hand, the snake profiles are characterized by a great variability of asymmetry (from 0.4 to 3.6 mg/cm^3) that cannot be explained only by the larger range of modal molecular weights of the samples (Fig. 2 and Table 1). On the other hand, the CsCl profiles for turtles, crocodilians and lizards have asymmetries in a narrower range, from 0.6 to 2.4 mg/cm^3. Higher values (>2 mg/cm^3) are found for the turtles, followed by the four crocodilians (1.5 to 1.9 mg/cm^3), their maximum value being reached by *Alligator mississipiensis*. Finally, the profiles of lizards are characterized by low (0.6 mg/cm^3 for *Podarcis muralis*) to intermediate asymmetries (1.3 mg/cm^3 for *Anguis fragilis*). As expected, the range of values observed for this parameter in each group of reptiles is essentially in agreement with the previously published data. In this study, however, we observed no asymmetries below 0.4 mg/cm^3, whereas in a previous study (Bernardi and Bernardi, 1990) lower asymmetries were observed for two snakes *Tomodon dorsatus* and *Dromicus poecilogyrus* (now called *Liophis poecilogyrus*).

3.3. Comparison with other vertebrate profiles

In order to compare the parameters obtained for reptiles and other vertebrates under the same conditions, we also investigated the CsCl profiles of two amphibians (*Rana esculenta*, *Xenopus sp.*), two birds (*Gallus gallus*, *Coturnix coturnix*) and a mammal (*Homo sapiens*). The two amphibians exhibited the expected low asymmetry (0.4 and 0.7 mg/cm^3) and heterogeneity (3.3 and 3.1 mg/cm^3; see Table 1), whereas the larger values obtained for human and two birds (2.3–3 for asymmetry and 5.6–6.4 for heterogeneity; see Table 1) confirmed previous data (Thiery et al., 1976; Bernardi et al., 1985; Kadi et al., 1993; Sabeur et al., 1993). Therefore, the range of asymmetry covered by the snake profiles goes from that observed for amphibians (with *Pliocercus euryzona* at 0.4 mg/cm^3) to that observed for human and birds (with *Lampropeltis triangulum polyzona* and *Lamprophis olivaceus* at 2.8 and 2.7 mg/cm^3, respectively). The same result was obtained for heterogeneity (see Table 1). Only one snake, *Aspidelaps lubricus*, shows surprisingly high values for both parameters that are perhaps overestimated because of a relatively low molecular weight of the DNA fragments (25 kb) or simply reflect peculiarities of this

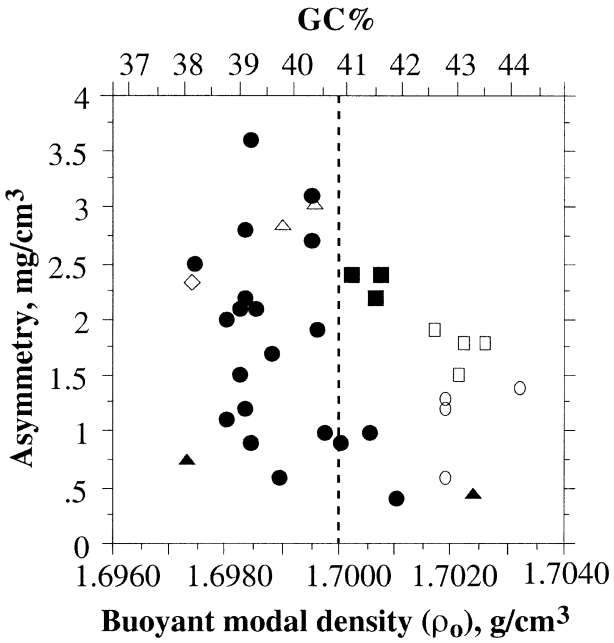

Fig. 3. Representation of the buoyant modal density (ρ_o) versus the asymmetry for the CsCl profiles obtained in this study. Symbols are as in Fig. 2.

genome. In contrast, the values obtained for the CsCl profiles of crocodilians and turtles were always lower than those of the two birds or human, but larger than those observed in amphibians.

4. Discussion

4.1. Mean and modal buoyant densities

The new data for reptiles are essentially in agreement with the previous results (Thiery et al., 1976; Bernardi and Bernardi, 1990), in which one can already recognize the peculiar position of snakes on the modal buoyant density axis, as well as the slight shift toward higher ρ_o values of the other groups, crocodilians and turtles. In the same way, the mean GC content obtained in this study for *Boa constrictor* (40.5%) is very similar to the value obtained by thermal denaturation (40.1%; Olmo and Odierna, 1977).

In the case of *Crocodylus niloticus*, however, the values obtained for the mean and modal buoyant density in this study are lower than the previous ones (Bernardi and Bernardi, 1990) and highly exceed the experimental error, which is considered to usually be ± 0.5 mg/cm^3 (Thiery et al., 1976) but is sometimes closer to ± 1 mg/cm^3. Moreover, the determination of the mean GC content for this species by the high-performance liquid chromatography technique (Jabbari et al., 1997) gives the same result as obtained in this study: 44.4% GC, equivalent to the $\langle\rho\rangle$ value 1.7036 g/cm^3 (Table 1).

4.2. Interspecific variability of asymmetry and heterogeneity among reptiles, especially snakes

The CsCl analyses of the snake genomes have shown a large variability in the profiles obtained, some appearing relatively homogeneous (*Dipsadinae*) and others relatively heterogeneous (such as *Lampropeltis triangulum campbelli*, *Lamprophis olivaceus*, *Notechis scutatus*). This is even more astonishing if we consider that these large differences sometimes occur in the same subfamily (*Colubrinae*).

It has been suggested, on the basis of previous profiles obtained for reptiles, that a major factor explaining this potential variability in the same group could be the presence or the absence of satellite DNAs (Bernardi and Bernardi, 1990). We have not observed a particular evidence for satellites (i.e. highly repetitive DNA, which is often visible as narrow bumps) in the CsCl profiles of reptiles. Nevertheless, the presence of cryptic satellites cannot be excluded, and there is a general tendency of such satellites to increase rather than decrease the heterogeneity and asymmetry in CsCl profiles (see Thiery et al., 1976; Macaya et al., 1976; Bernardi and Bernardi, 1990; Sabeur et al., 1993; Kadi et al., 1993, for examples). Similarly, some thermal denaturation studies have shown that the proportion of repetitive elements can vary significantly among the genomes of snakes (Olmo et al., 1981, 1985). However, such variations in repetitive DNA were also detected in lizard genomes (Olmo et al., 1981, 1985) although no large variability in the shapes of the profiles have been noticed in this group so far. In summary, it is difficult to estimate the real contribution of interspersed repeats and satellite repeats to the variability we observed among snake genomes.

The unusual variability of compositional asymmetry and heterogeneity within the *Colubridae* may be also partially linked to the fact that colubrids are the most species-rich reptile family. This family contains about 1800 species (snakes are estimated to comprise 2900 species, according to the EMBL Reptile Database) which are distributed all over the world in almost all possible habitats. Moreover, the systematics for this group are still far from satisfactory, and some of the differences observed within a subfamily could also be the result of incorrect taxonomy that reflects phylogenetic uncertainties. Indeed, the times of divergences for snakes are not well resolved, even if their origin is generally estimated at 125 million years ago (Benton, 1990). Except for the points mentioned above, we have not been able to identify any particular characteristic that distinguishes homogeneous from heterogeneous species.

Finally, it cannot be completely ruled out that technical difficulties may be responsible for some of the differences in snake heterogeneity and asymmetry that we observed. Such difficulties could include nonlinear baselines (e.g. due to minor contaminants) leading to artifactual widening or truncation of the profile, or the possible presence of very small, $\ll 1$ kb fragments in some DNA samples (e.g. due to snakes' especially strong DNase activities; G. Bernardi, unpublished observations) that could escape quantification on gels, thus cryptically augmenting the profile broadening (which increases tenfold when the fragment size decreases from 10 kb to 100 bp, see Section 2.3).

4.3. Comparison with other vertebrates

When all the profiles available for vertebrates in the literature are considered, the range of modal buoyant density observed for snakes appears very similar to that of most mammals and birds (for the latter, see Sabeur et al., 1993; Kadi et al., 1993; Douady et al., 2000 and references therein). On the contrary, crocodiles, turtles and lizards show a shift toward higher values that is also observed in the case of some mammals, the murids (see Douady et al., 2000, and references therein). The fishes are the only group of vertebrates for which the ρ_o range is very large (1.6950–1.7080 g/cm^3).

For many reptiles (turtles and crocodilians, some snakes and lizards), the asymmetry parameter observed was intermediate between the values obtained for fishes and amphibians and those of birds and mammals. This observation is in agreement with other studies that conclude an intermediate status of reptiles with respect to different parameters that are generally characteristic of mammals and birds, such as the level of methylation (Jabbari et al., 1997), the base

composition at the coding sequence level (Hughes et al., 1999), or the presence of R-bands (although faint compared with those of mammals; Schmid and Guttenbach, 1988) and the absence of T-bands (Michael Schmid, personal communication). While some properties such as genome size appear more similar to birds and mammals (Olmo et al., 1989), other properties such as the process for regulating body temperature are similar (although not identical, cf. Guibé, 1970) to those in fishes and amphibians.

In conclusion, the results of our wide taxonomic sampling of reptiles indicate a great variability of compositional heterogeneity among snake genomes, with some homogeneous and some heterogeneous species, whereas the crocodilian and turtle genomes analysed confirm an intermediate compositional pattern, more heterogeneous than fishes and amphibians but less heterogeneous than birds and mammals.

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