



Afrotheria genome; overestimation of genome size and distinct chromosome GC content revealed by flow karyotyping



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ARTICLE INFO

Article history:

Received 21 June 2013

Accepted 13 September 2013

Available online 19 September 2013

Keywords:

Genome size

GC content

Afrotheria

Genome evolution

Chromosome profile

ABSTRACT

Afrotheria genome size is reported to be over 50% larger than that of human, but we show that this is a gross overestimate. Although genome sequencing in Afrotheria is not complete, extensive homology with human has been revealed by chromosome painting. We provide new data on chromosome size and GC content in four Afrotherian species using flow karyotyping. Genome sizes are 4.13 Gb in aardvark, 4.01 Gb in African elephant, 3.69 Gb in golden mole and 3.31 Gb in manatee, whereas published results show a mean of 5.18 Gb for Afrotheria. Genome GC content shows a negative correlation with size, indicating that this is due to differences in the amount of AT-rich sequences. Low genome GC content and small variance in chromosome GC content are characteristic of aardvark and elephant and may be associated with the high degree of conserved synteny, suggesting that these are features of the Afrotherian ancestral genome.

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1. Introduction

Comparative genomic studies on Afrotheria, the most basal mammalian lineage and distinct by molecular genetic studies from other eutherian mammals, can lead to an improved understanding of mammalian genome evolution [1]. Whole genome comparisons between human and Afrotheria have been made by chromosome painting, indicating extensive conservation and suggesting a presumptive eutherian ancestral karyotype of $2n = 44$ or $2n = 46$ [2–4]. However, the Afrotheria genome has not been fully characterised by sequencing, although this is currently underway in three species; lesser hedgehog tenrec, hyrax and African elephant.

Mammalian karyotypes are highly rearranged throughout evolution and show a great diversity in chromosome number and form [5]. Despite long divergence times, chromosome homology revealed by reciprocal painting displays almost one-to-one correspondence between human, aardvark and African elephant except for heterochromatic regions [2]. It is suggested that chromosome banding patterns are highly conserved within mammals and that all mammals have similar genome sizes after the subtraction of the heterochromatin component [6]. However, conventional cytogenetic studies based on qualitative analysis cannot detect intrinsic differences between homologies because of their low resolution.

Genome size is fundamental to genome structure and characterises each species. A large number of genome size data have been accumulated in the genome size database [7], showing extensive variation in mammals. A previous study on Afrotheria reported that the mean

genome size measured on Feulgen-stained nuclei was 5.5 pg, i.e. more than 50% higher than that of humans, suggesting that there were significant size differences between Afrotheria and other eutherian clades except for Xenarthra [8]. However, discrepancies between different estimates of genome size for the same species have been reported due to methodological problems [9]. This implies that the database contains inaccuracies and that more precise measurements of genome size are needed for meaningful comparisons.

An early analysis of aardvark chromosomes on photographic images measured the length of each chromosome arm [10], estimating, for example, that the proportion of chromosome 1 is approximately 20.5% of the genome. The aardvark genome size measured by microdensitometer was 1.67 times larger than that of human [10]. Applying this to the human genome size, 3.15 Gb as measured from the flow karyotype, aardvark chromosome 1 is calculated to be 1078 Mb, equivalent to the chicken total genome size. Chromosome painting has shown that aardvark chromosome 1 is homologous to 6 human chromosomes/regions 2pter-q13, 4, 8p, 13, 16q and 19q [2]. We estimate that the size of these homologous regions in the human karyotype is 520 Mb from sequence data, indicating that the aardvark chromosome 1 is 2.07 times larger than its human homologues if the previous data are accepted. It is questionable whether the extensive homology between human and Afrotheria is consistent with such a remarkably large genome size.

Flow karyotyping has revealed chromosome sizes in zebrafish [11], chicken, turtle, crocodile [12], bat [13], dog [14] and human [15], leading to estimations of genome size. Most data included in the database do not show the sex of samples and ignore the difference between males and females in each species. Chromosome measurements distinguishes sex differences in genome sizes by determining the size of individual sex

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chromosomes [12–15], allowing comparison between species, an important factor in considering X chromosome conservation during mammalian evolution.

Although some attention has been paid to Afrotherian genomes, genetic information is still lacking. In this study we determine the individual chromosome size and GC content of four Afrotherian species, armadillo (*Orycteropus afer*, OAF), African elephant (*Loxodonta Africana*, LAF), manatee (*Trichechus manatus latirostris*, TMA) and golden mole (*Chrysochloris asiatica*, CAS) from flow karyotypes and find that their genome sizes have been seriously overestimated.

2. Results

The 11 OAF, 29 LAF, 25 TMA and 15 CAS chromosomes were resolved into 11, 23, 19 and 12 peaks, respectively, because some peaks included two or three chromosomes of similar size and GC content and so could not be distinguished in the flow karyotypes [2,16,17]. Each chromosome size and GC-content was estimated from the flow karyotype using human chromosomes 4, 17 and 19 as references (Table 1). Chromosome profiles for each species based on size and GC content are shown in Fig. 1. The variance in chromosome GC content excluding the Y chromosome is 1.83 for OAF, 0.75 for LAF, 1.81 for TMA and 3.13 for CAS.

The total genome sizes were 4132 Mb for OAF, 4006 Mb for LAF, 3308 Mb for TMA and 3690 Mb for CAS, calculated from the sum of individual chromosome sizes excluding the Y chromosome (Table 1), indicating that the previous study overestimates these sizes by 41, 10, 40 and 70% respectively. Our results show that the size relative to the human genome (3.15 Gb) is 131% for OAF, 127% for LAF, 105% for TMA and 117% for CAS. The sizes in human regions homologous to each OAF chromosome and the proportion of chromosomal DNA in each genome are shown in Table 2. The total GC content is 39.5% for

Table 1
Size and GC content of each chromosome and each total genome (TG). The lowest and highest GC content in each genome are shown in bold italics (excluding Y chromosome).

Chr	Armadillo		Elephant		Manatee		Golden mole	
	Size (Mb)	GC (%)	Size (Mb)	GC (%)	Size (Mb)	GC (%)	Size (Mb)	GC (%)
1	740	38.6	258	38.0	232	39.6	529	40.6
2	686	38.8	244	39.8	205	41.4	506	40.5
3	558	39.3	259	38.0	201	39.6	416	41.5
4	440	39.3	212	38.0	205	41.3	274	41.9
5	415	39.3	212	38.0	207	38.7	274	41.9
6	339	40.0	177	38.2	181	39.9	219	41.8
7	294	39.9	162	38.5	201	39.6	222	41.5
8	237	41.1	153	37.7	150	40.9	204	41.2
9	121	43.2	137	38.1	126	43.0	200	41.8
10			138	38.9	154	39.5	171	41.7
11			114	40.9	125	41.0	148	44.0
12			127	39.2	114	41.0	124	46.6
13			147	39.5	123	40.4	105	44.5
14			127	39.2	83	41.3	95	45.1
15			113	37.9	123	39.2		
16			127	37.9	111	40.0		
17			119	38.8	92	42.2		
18			106	39.4	87	40.0		
19			100	38.6	82	40.7		
20			106	39.4	86	44.6		
21			101	37.3	90	41.5		
22			100	38.6	90	39.2		
23			88	40.1	59	41.7		
24			65	39.5				
25			95	39.7				
26			95	37.6				
27			70	38.4				
X	301	40.4	198	38.2	181	39.9	202	41.8
Y	135	38.3	56	41.5	38	42.0		
TG	4132	39.5	4006	38.7	3308	40.5	3690	41.7
Variance		1.83		0.75		1.81		3.13

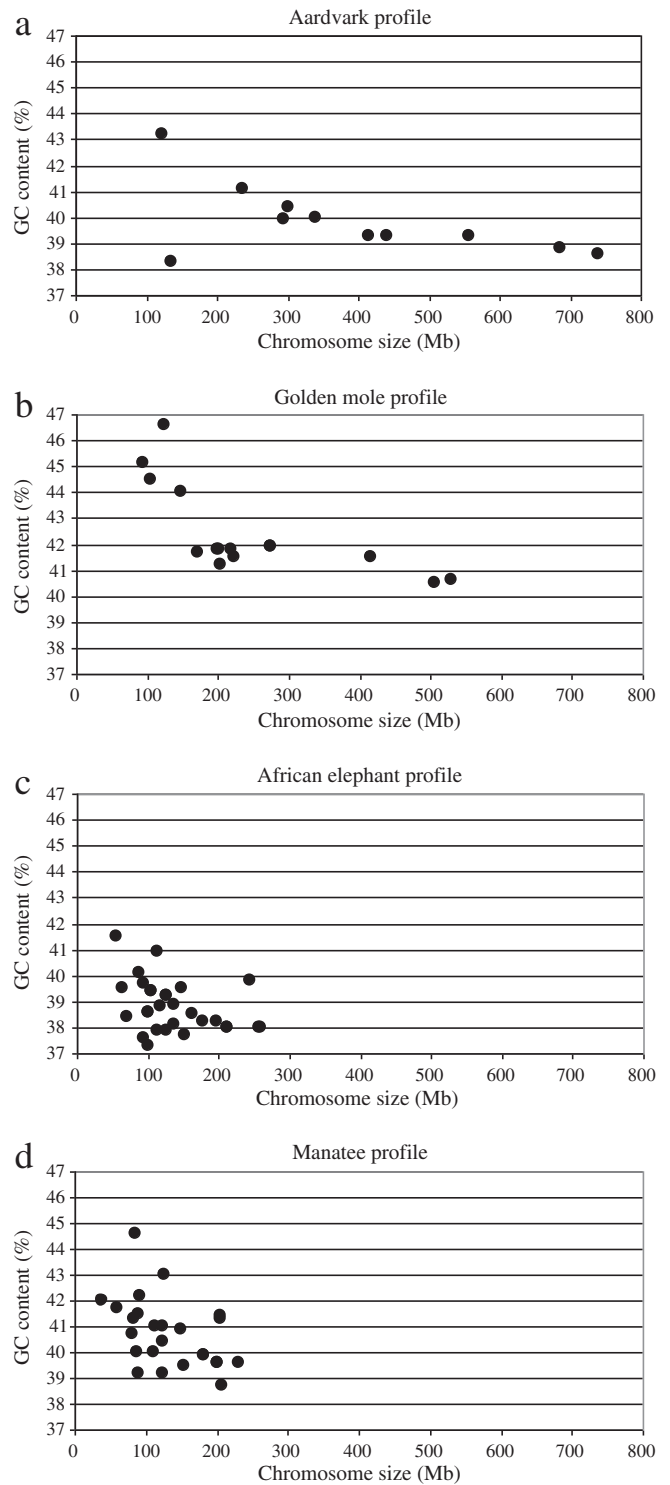


Fig. 1. Chromosome profiles showing the relationship between chromosome size and GC-content in the armadillo (a), golden mole (b), African elephant (c) and manatee (d) based on measurements from flow karyotypes. The golden mole and manatee are similar to the armadillo and elephant respectively, but have elevated GC content.

OAF, 38.7% for LAF, 40.5% for TMA and 41.7% for CAS (Table 1), and its relationship to genome size is shown in Fig. 2.

3. Discussion

The total genome sizes in Afrotherian species measured from flow karyotypes are between 3.3 and 4.1 Gb (Table 1), up to 30% larger

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