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An analysis of trypanosomatids kDNA minicircle by absolute dinucleotide frequency

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ABSTRACT

Trypanosomatid mitochondrial DNA (kDNA) possesses thousands of copies of small circular molecules called minicircles. Due to a high level of nucleotide polymorphism among copies, sequence alignment for species or strain characterization is not appropriate. In this work we report dinucleotide absolute frequency as a method to analyze minicircle sequences heterogeneity in trypanosomatids. Using *Trypanosoma rangeli* and *Leishmania guyanensis* minicircles as example of sequence length heterogeneity, we show that dinucleotide frequency of minicircles whose length variation is less than to 10% is relatively constant. Dinucleotide frequencies in *Leishmania* genus point out three clusters of predominant dinucleotide profiles: GG/TT/TG for Old World species; ii) TT/AA/TA for New World species and iii) TT/GG(AA) TA(AT) for *Sauroleishmania*. *Trypanosoma* species displayed broad range composition and the highest frequency values. Their dinucleotide profile appears to be species specific, except for African trypanosomes which exhibit similar composition. The low number of sequences from *Crithidia*, *Herpetomonas*, *Phytomonas* and *Wallaceina* did not allow a generalized analysis, however some species present highly similar compositional profile, e.g., *Wallaceina* species. Distinct signatures for Trypanosomatidae family members can be generated by using values of absolute frequencies, range and composition of most/least frequent dinucleotides from minicircles. Each species can be graphically represented by a diagram of frequencies along with a box plot of summary statistics.

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1. Introduction

Trypanosomatidae family includes flagellated protozoa parasites that can be assembled into two groups according to the number of hosts in their life-cycle: monoxenous (only one host) and dixenous (two hosts, invertebrate and vertebrate or plant) [1]. The first group comprises species from genera *Blastocrithidia*, *Crithidia*, *Herpetomonas*, *Leptomonas*, *Wallaceina* and *Sergeia*, whereas the second one embraces genera *Leishmania, Sauroleishmania, Trypanosoma* and *Phytomonas* [1]. Recently the genera *Angomonas* and *Strigomonas*, which include symbiont-harboring trypanosomatids, have passed through a phylogenetic validation [2]. Meanwhile, two other genera have been challenged on their current status: *Rhynchoidomonas*, which lacks molecular evidence to confirm its taxonomic positioning, and *Endotrypanum*, which is not considered a valid genus after phylogenetic analysis pointed out its close relatedness to *Leishmania* [1]. These protozoa present a particular organization of mitochondrial DNA (also known as kinetoplast DNA or kDNA), located next to flagellar pocket in a unique and large mitochondria. kDNA accounts for 20% of total DNA in the cell [3] and is composed by two different types of circular molecules, termed maxicircles and minicircles. Minicircles have length ranging from 0.6 to 10 Kb [4], are heterogeneous in sequence and present ca. 5000 copies per kDNA network [5]. The maxicircle component of the kDNA encodes protein-coding genes and ribosomal RNAs. The transcripts of the former genes undergo the uridine insertion/deletion form of RNA editing [3], leading to translatable mRNAs. Information for the number of uridines inserted and/or deleted is provided by a large set of guide RNAs, encoded by the minicircle component of the kDNA [6]. Redundancy in gRNA number could explain the complexity observed in minicircle sequences [7]. Peculiarities in minicircle composition and structure, such as symmetrically disposed variable regions and highly conserved 12 bases sequences (GGGGTT GGTGA, the Universal Minicircle Sequence — UMS) allowed the development of molecular methods for typing and diagnosis of trypanosomatids [8–12]. They have also been used as information source to address the taxonomic challenges of trypanosomatids [13–18]. However kDNA sequence analysis of large data set has faced limits using alignment tools [9,12,15,17,19–21]. To circumvent the restriction of methods based on minicircle sequences plain alignment, we analyzed dinucleotide composition of full length minicircles from several members of Trypanosomatidae family. The nucleotide composition of both eukaryotic and prokaryotic organisms has been demonstrated to be specific to a particular genome, leading to the concept of genome signature [22–28]. Applications of this method include evolutionary distances and similarity analysis and most works report on di, tri and tetra nucleotides relative frequency from partial or whole genomes [22,23,25,27]. In general the main target of nucleotide composition analysis is the nuclear genomic

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sequences, but the mitochondrial DNA has been used as well [26–28]. The drawback of dinucleotide frequency analysis is the graphical presentation of the obtained information. In general, works reporting on dinucleotide frequency have relied on tables to describe variability in sequence composition [22,26].

Through the use the of dinucleotide composition as a tag we show here that the absolute frequency of 16 dinucleotides may be used to establish a relationship between kDNA minicircle composition and interspecific analysis in Trypanosomatidae family.

2. Methods

2.1. Data source

We have used trypanosomatid minicircle sequences available in GenBank — NCBI. They were converted to Fasta format, and inspected for the presence of Universal Minicircle Sequence (UMS, the 12mer GGGGTTGGTGA) to determine the kDNA origin of the sequence. Table 1 lists the amount of minicircle sequences, the highest available

Table 1
List of minicircle sequences, their length and respective accession numbers.

Species	UMS	Maximum size (bp)	Accession numbers
Trypanosoma cruzi	4	1451	U07846, U07845, X04680, M15512, M15511, M18816, M18815, M18814
T. rangeli	2	1764	L28039, L28038, L19395, L19391, L19388
T. equiperdum	2	1012	EU155059, EU155057, EU155060, EU155058, AY311485, V01395, M14763
T. brucei	1	1058	L25588, L11652, EU155056, AY770509, AY698074, AY770510, AY770508, V01389, V01388, U03908, M15324, M15323, M15322, M15321, L25589
T. evansi	1	1001	AY557604, AY918061, M57462, M57461, M57460, M57459, AY698076, AY557604, AY918061, AY698075, M33751, M34848
T. avium	1	827	AF027214
T. congolense	1	964	M19750, M19751
T. carassii	2	1599	S82304
T. lewisi	2	1018	M17995, M17996
Crithidia oncopelti	1[a]	1848	X17109
C. fasciculata	2	2515	M19266, U12625
Herpetomonas samuelpessoai	2	1274	AF064359
Phytomonas serpens	2[a]	1476	AF034624, AF034625
Phytomonas sp.	2[a]	1604	AF397906, M74195
Wallaceina brevicula	2	1477	Z32854
W. inonstans	2	1494	AF121798, AF124056
Leptomonas collosoma	2	2457	DQ239763, DQ239762
Leishmania archibaldi	1	710	AF308688
L. infantum	1	818	Z35501, Z35500, AJ275335, AJ275333, AJ275331, AJ275329, AJ275327, AJ275321, AJ275334, AJ275332, AJ275330, AF027578, AF169139, AF169133, AF169140, AF169131, AF190476, AF188701, AF184044, AF190475, AJ270144, AF190883, AF190882, AF103741, AF103735, AF103740, AJ223724, Z35292, Z35273, Z35272, Z35269, Z35274, Z35270, Z35271
L. donovani	1	833	AF399822, AF184892, AF169136, AF169135, AF169134, AF168358, AF168357, AF168356, AF167715, AF167714, AF167713, AF167712, AF167718, AF167717, AJ270145, AF103737, AF103736, AF103742, AJ010082, AJ010080, AJ010079, AJ010076, AJ010074, AF239704, AF239703, AF239702, AJ010083, AJ010075, AJ010077, AJ010084, Z35275, Y11402, Y11401, AJ010087, AJ010086, AJ010085, AJ010081, AJ010078, L19877
L. major	1	728	AF308685, J04654, AB678349, AF515558, HQ727557, HQ727555, HQ727556, HQ727554, HQ727552
L. tropica	1	747	AF308690, AF308689
L. chagasi	1	807	AF169138, AF169132, AF103739, AF169137, AF103738, Z35276
L. amazonensis	1	859	M94089, M94088
L. mexicana	1	859	AY145437, AF541871, Z11556, Z11554, Z11555, Z11553, Z11552, Z11551, Z11550, Z11549
L. braziliensis	1	749	M87315, U19803, U19806, U19807, U19805
L. guyanensis	1	858	M87316, AF130467
L. panamensis	1	751	AF118474, AF118472, AF118470, AF118468, AF118466, AF118464, AF118462, AF118460, AF118458, AF118456, AF118454, AF118473, AF118471, AF118469, AF118467, AF118465, AF118463, AF118461, AF118459, AF118457, AF118455, AY366071
L. peruviana	1	751	M87317
L. lainsoni	1	754	AF088234, AF088232, AF088230, AF088228, AF088226, AF088235, AF088233, AF088231, AF088229, AF088227, AF088225
L. tarentolae	1	914	X60510, X60508, AF380737, AF380736, AF380735, AF380734, AF380733, AF380732, AF380731, AF380730, AF380729, AF380728, AF380727, AF380726, AF380725, AF380724, AF380703, AF380702, AF380700, AF380699, AF380698, AF380697, AF380696, AF380695, AF380694, AF380693, AF380691, AF380690, AF380689, AF380688, AF380687, AF380686, AF380685, AF380684, AF380683, AF380682, AF380681, AF380679, AF380678, AF380677, AF380676, AF380675, AF380674, AF380753, AF380752, AF380751, AF380750, AF380749, AF380748, AF380747, AF380746, AF380745, AF380744, AF380743, AF380742, AF380741, AF380740, AF380739, AF380738, AF380723, AF380722, AF380721, AF380720, AF380719, AF380718, AF380717, AF380716, AF380715, AF380714, AF380713, AF380712, AF380711, AF380710, AF380709, AF380708, AF380707, AF380706, AF380705, AF380704, K01980, K01979, K01978
L. gymnodactyli	1	875	Z32856, Z32855
L. guliki	1	860	Z32857
L. aethiopica	1	864	U77892

[a] Similar but not identical to UMS (UMS: Universal Minicircle Sequence or 12mer).

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