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Research paper

A genome survey sequencing of the Java mouse deer (*Tragulus javanicus*) adds new aspects to the evolution of lineage specific retrotransposons in Ruminantia (Cetartiodactyla)

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ABSTRACT

Ruminantia, the ruminating, hoofed mammals (cow, deer, giraffe and allies) are an unranked artiodactylan clade. Around 50–60 million years ago the BovB retrotransposon entered the ancestral ruminantian genome through horizontal gene transfer. A survey genome screen using 454-pyrosequencing of the Java mouse deer (*Tragulus javanicus*) and the lesser kudu (*Tragelaphus imberbis*) was done to investigate and to compare the landscape of transposable elements within Ruminantia. The family Tragulidae (mouse deer) is the only representative of Tragulina and phylogenetically important, because it represents the earliest divergence in Ruminantia. The data analyses show that, relative to other ruminantian species, the lesser kudu genome has seen an expansion of BovB Long INterspersed Elements (LINEs) and BovB related Short INterspersed Elements (SINEs) like BOVA2. In comparison the genome of Java mouse deer has fewer BovB elements than other ruminants, especially Bovinae, and has in addition a novel CHR-3 SINE most likely propagated by LINE-1. By contrast the other ruminants have low amounts of CHR SINEs but high numbers of actively propagating BovB-derived and BovB-propagated SINEs. The survey sequencing data suggest that the transposable element landscape in mouse deer (Tragulina) is unique among Ruminantia, suggesting a lineage specific evolutionary trajectory that does not involve BovB mediated retrotransposition. This shows that the genomic landscape of mobile genetic elements can rapidly change in any lineage.

1. Introduction

Ruminantia consists of nearly 200 species some of which, due to their domestication, are economically very important (Hernández Fernández and Vrba, 2005). Ruminantia comprises the two infraorders Tragulina and Pecora. Tragulina consist of ten species, whose ancestors diverged before the evolution of the characteristic bony growths on the skull found in Pecora (Nowak, 2005). Tragulina includes some of the smallest living ruminantian species, such as the Java mouse deer (Nowak, 2005). Pecora is characterized by the phenotypic horns, antlers and ossicones and contains the most important livestock species such as cow, sheep, goat and deer, but also the musk deer, the pronghorn and the iconic African species like giraffe, antelopes and kudu (Fig. 1) (Nowak, 2005; Groves and Grubb, 2011). Ruminant genomes, like mammalian genomes in general, contain a high fraction of transposable elements (TEs) (e.g. Lander et al., 2001; Adelson et al., 2009; Elsik et al., 2009; McGowen et al., 2012). Among the mammalian transposable elements retrotransposons comprise mainly Short INterspersed Elements (SINEs), Long INterspersed Elements (LINEs) and Endogenous RetroViruses (ERVs) (Goodier and Kazazian, 2008). In the well-studied cow genome 96% of TEs are retrotransposons that propagate via RNA intermediates (copy-and-paste), and only 4% of TEs are DNA transposons that propagate by a cut-and-paste mechanism (Adelson et al., 2009; Elsik et al., 2009).

A curiosity of the cow genome is that approximately one quarter is derived from a horizontal transfer of a BovB LINE (Adelson et al., 2009; Elsik et al., 2009) into the ancestral ruminant genome (Fig. 1). The BovB LINE was probably transferred from reptiles, likely mediated by a parasitic vector 50–60 million years ago (mya) (Szemraj et al.,

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Abbreviations: A (nucleotide), adenosine; Ala, alanine; ALPINE, alpaca SINE; BDDF, bovine dimer driven family; BLAT, blast like alignment tool; BLAST, *basic local alignment search tool*; BovB, bovine RTE element; BWA, Burrows–Wheeler aligner; C (nucleotide), Cytosine; CHR SINE, Cetacea, Hippopotamidae and Ruminantia SINE; DNA, deoxyribonucleic acid; et al, et alii/et aliae/et alia; ERV, Endogenous Retrovirus; Fig, figure; Glu, glutamic acid; Kb, kilo bases; LINE, Long INterspersed Elements; LTR, long terminal repeat; mt, mitochondrial; mya, million years ago; NCBI, National Center for Biotechnology Information; nt, nucleotide; numts, nuclear mitochondrial sequences; PRE-SINE, a swine SINE; RNA, ribonucleic acid; RTE, retrotransposons like element; SINE, Short INterspersed Elements; SINE_VV, SINE of *Vicugna vicugna*; Supp, supplementary; TE, transposable element; Thr, threonine; tRNA, transfer RNA; Vic-1, vicuna SINE 1.

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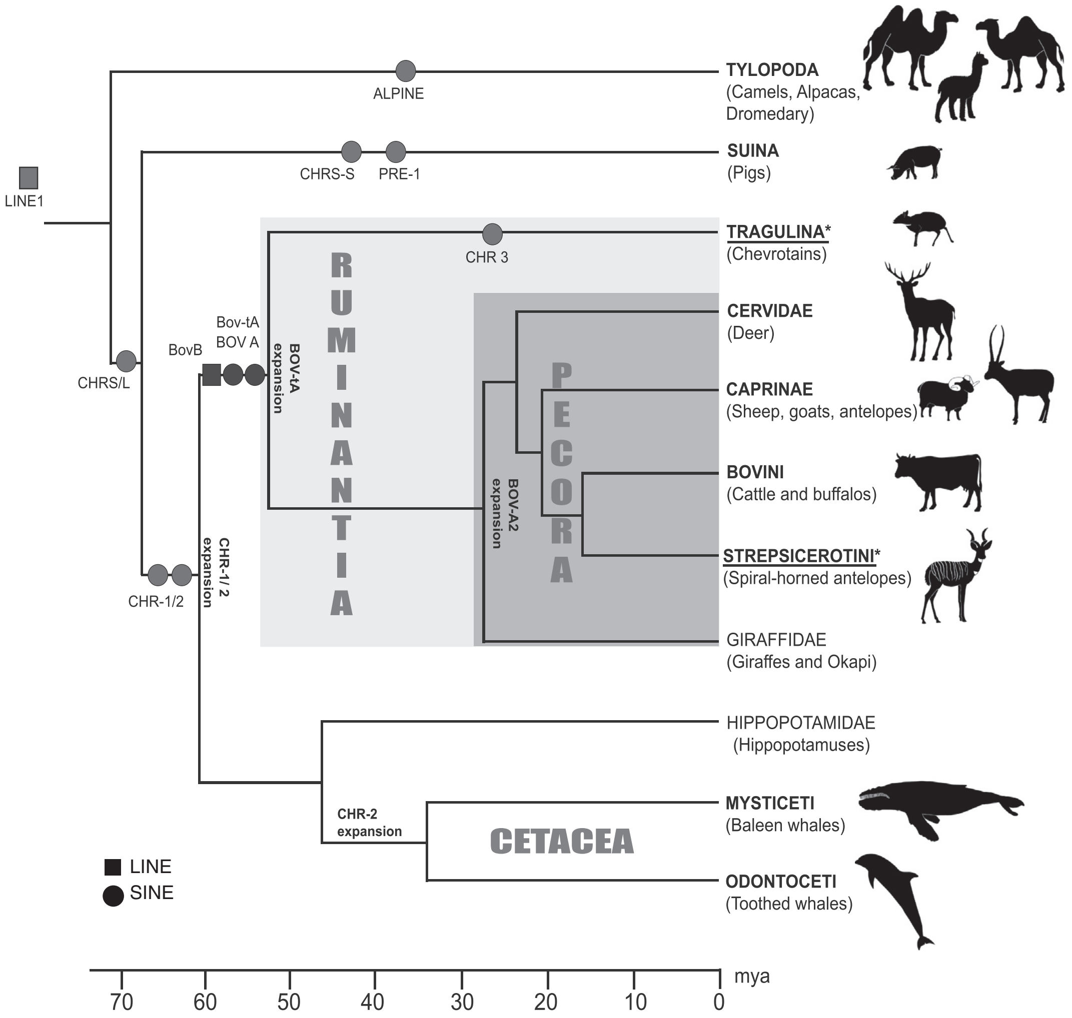

Fig. 1. Evolution and occurrence of SINEs related to CHR and BovB plotted on a phylogenetic tree of Cetartiodactyla. Squares indicate autonomous LINEs and circles depict non-autonomous SINEs. All CHRs share the tRNA-Glutamine related 5′-part and a poly(A)tail region. The CHR families are shown at the point of expected first occurrence. Most CHRs have an additional short 5′ sequence and differ in length of the sequence upstream the poly(A)tail. CHRS and CHRL are assumed to be the most ancestral CHR types. CHR-1 SINEs can be divided into three subgroups (CHR-1-I to III) with III being precursor to the CHR-2 elements. CHR-2 is grouped into CHR-2 A-F with additional species-specific subgroups (indicated as "expansion"). Suina and Tylopoda (camels) have additional SINEs. PRE-1 is characteristic for Suina and derived from tRNA Threonine. Camels have the tRNA Alanine derived ALPINE. The ruminant Bov-tA SINEs may result from recombination of Bov-A, a truncated BovB, and CHR-2 (Nikaido et al., 2001; Shimamura et al., 1999). The Tragulina (chevrotains) have the lineage specific CHR-3 SINE. CHR-3 shares tRNA-Glu part and the segmental duplicated part with CHR-2, but differs in the number of segmental duplications, and contains a region not shared with any other CHR. The tree is constructed and scaled according to Hallström et al. (2011) and Hassanin et al. (2012). The two newly sequenced low-coverage genomes are underlined and indicated by an * next to the name. All taxa included in the study are represented by a shadow figure next to their names.

1995; Youngman et al., 1996; Kordiš and Gubenšek, 1997, 1998, 1999a, b; Župunski et al., 2001, Piskurek et al. 2007, Walsh et al., 2013). The BovB LINEs have been extensively studied in the cow genome and are reported in earlier publications as BDDF, ART-2 or Pst elements (for review see Kordiš and Gubenšek, 1999b). This element is part of the RTE (RetroTransposable Element) clade of non-LTR retrotransposons and is also referred to as RTE elements (Youngman et al., 1996; Malik and Eickbush, 1998). Due to its high abundance, BovB has had a major impact on the ruminant genome and its genome structure (Kordiš and Gubenšek, 1999a, 1999b; Adelson et al., 2009). New SINEs emerged in Ruminantia after the BovB invasion through recombination of BovB with the tRNA related region of the existing SINEs (Bov-tA) or dimerization of the tail-region of Bov-tA (BOVA2) (Okada and Hamada, 1997; Shimamura et al., 1997, 1999) (Supp. Fig. 1).

While the TE landscape has been characterized for some pecoran species (i.e. cow, sheep) (Adelson et al., 2009; Jiang et al., 2014), it is not known, if the earliest divergence among ruminants, Tragulina, shares the same set of TEs. Previous studies have found evidence of a mouse deer-specific SINE, but to date no formal descriptions of its properties, abundance and occurrence have been made (Iwashita et al., 2006; Iwashita and Kordiš, 2006; Nilsson et al., 2012). The presence of a mouse deer specific SINE suggests that the mouse deer TE landscape might hold additional novelties.

In all mammals SINEs are propagated in the genome by the retrotransposition machinery encoded by the autonomous LINE elements. Different SINE types are usually order-specific e.g. Alu elements in primates or SINEC in Carnivora (Kramerov and Vassetzky, 2011). Within Cetartiodactyla the characteristic CHR SINE family has been identified in Cetacea, Hippopotamidae and Ruminantia (accordingly named CHR) and is very abundant with numerous CHR sub-families (Shimamura et al., 1999) (Fig. 1, Supp. Fig. 1). CHR SINEs are composed of a tRNA-Glu related 5′ part, a tRNA-unrelated domain, a poly(A)tail and are flanked by diagnostic target site duplications (TSD) indicating a propagation in the genome via the autonomous LINE-1 (Roy-Engel et al., 2002). The CHRs and BovB related SINEs (BOVA2, Bov-tA) have been valuable phylogenetic markers in numerous studies to resolve the phylogenetic relationships among Cetartiodactyla (Shimamura et al., 1997; Nomura et al., 1998; Nikaido et al., 1999, 2001; Nijman et al., 2002; Nilsson et al., 2012).

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