

The Phylogeny of the Cetartiodactyla Based on Complete Mitochondrial Genomes

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Abstract

Efforts have been made to investigate the phylogeny of Cetartiodactyla; however, the relationships within this group still remain controversial. Due to the limitation of collecting samples from some key species of the Cetartiodactyla, it is difficult to perform molecular phylogenetic analysis to find out their precise classification scheme. Fortunately, much up-to-date, more molecular data samples of this group are available from GenBank. To further clarify the relationships within the Cetartiodactyla, phylogenetic analyses of the Cetartiodactyla were conducted using Bayesian and maximum likelihood (ML) methods based on complete mitochondrial genomes. The results indicate that Moschidae sister to Bovidae, and recognize the families Moschidae, Bovidae, Cervidae and Giraffidae to be four monophyletic groups. Phylogenetic trees also indicate that the basal divergence within the Cetartiodactyla is between the Suina and a strongly supported clade of the remaining Cetartiodactyla; Tragulidae is the early offshoot within the Ruminantia, followed by the Antilocapridae.

Keywords: molecular phylogeny, cetartiodactyla, mitochondrial genome

1. Introduction

Over the last 150 years, Artiodactyla has been regarded as a single origin and was usually classified into three main suborders: Ruminantia, Tylopoda, and Suiformes (Simpson, 1945). Recent works suggest a close relationship between Artiodactyla and Cetacea based on a host of paleontological (Thewissen & Hussain, 1993), morphological (Thewissen et al., 2001), and molecular (Murphy et al., 2001; Hassanin et al., 2012) studies. Concurrently, molecular data analyses designate that the Cetacea sister to Hippopotamidae (Murphy et al., 2001; Nikaido et al., 1999), which contradicted with the traditional monophyly of Artiodactyla and suggested to put all species of Artiodactyla and Cetacea into a single order, called Cetartiodactyla (Montgelard et al., 1997). Forefore, Cetartiodactyla comprises of all the species from Cetacea, Hippopotamidae, Antilocapridae, Bovidae, Cervidae, Giraffidae, Moschidae, Tragulidae, Suidae, Tayassuidae and Camelidae. However, phylogenetic relationships of Cetartiodactyla still remain ambiguous. For instance, the issue about what is the root of Cetartiodactyla is unresolved (Gatesy et al., 2002; Ursing et al., 2000). And historically, there were three hypotheses: a basal position for the Suina (Matthee et al., 2001) or Tylopoda (Gatesy et al., 1999; Zhou et al., 2011) or a paraphyly of Tylopoda and Suina (Arnason et al., 2000) as a sister group to Cetruminantia (Ruminantia + Cetacea + Hippopotamidae). Although Tylopoda hypothesis was favoured by most molecular studies (Nikaido et al., 1999; Agnarsson & May-Collado, 2008; Murphy et al., 2001), it was not proven perfect by rigorous statistical testing in most cases (Shimodaira et al., 2002). And these studies did not reject the other two alternative topologies at a significant statistical level (Ursing et al., 2000). Moreover, though the Tylopoda hypothesis was widely accepted, Bayesian inference methods dependent on cytochrome b sequences, suggested a sister group relationship between Suina and Ruminantia (Agnarsson & May-Collado, 2008). Even though supertree analyses, utilizing the supermatrix with maximum parsimony (MRP) (Ragan, 1992), can present respective results of these hypotheses, such conclusions can usually reach no consensus among phylogeny studies (Beck et al., 2006; Gatesy et al., 2002; Price et al., 2005). For instance, Gatesy et al. (2002) suggested Tylopoda and Suina as the earliest diverged group, but Price et al. (2005) determined an early divergence of Tylopoda with additional taxon sampling.

The place of Moschidae (musk deer) within Ruminantia is controversial. Although Moschidae is widely recognized as a monophyletic family (Flerov, 1952; Janis & Scott, 1988; Li et al., 1998), the interrelationships

and the phylogenetic position among Ruminantia families are cause for long-standing disputes. Phylogenetic relationships among Cervidae, Moschidae and Bovidae have been investigated using both mitochondrial and nuclear sequences (Su et al., 2001; Matthee et al., 2001; Guha et al., 2007). However, these studies have not conclusively resolved the phylogenetic position of Moschidae. Here, we conducted phylogenetic analyses within Cetartiodactyla based on complete mitochondrial genomes, which will improve our understanding of evolution biology of this mammal group.

2. Methods

In this study, all of the complete mitochondrial genomes were downloaded from GenBank, and the 12 heavy-strand encoded protein-coding genes were aligned according to Nikaido et al. (2001). After deletion of gaps and ambiguous sites adjacent to gaps, 10,761 nucleotides were obtained. Multiple alignments of the 12 concatenated protein-coding genes of 50 species (Table 1) were performed using ClustalX (Tompson et al., 1997) with the default setting. Two species of Perissodactyla were used to root the tree of Cetartiodactyla (Table 1). Bayesian phylogenetic analysis (BI) was conducted using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). The best-fit model (GTR+I+G) of sequence evolution for Bayesian analyses was obtained by Modeltest 3.7 (Posada & Crandall, 1998) under the Akaike Information Criterion (AIC). Four independent Markov chains Monte Carlo (MCMC) ran simultaneously for ten million generations, sampling one tree per 200 generations, and discarding the first 25% of samples as the burn-in. Tracer v1.3 (Rambaut & Drummond, 2005) was used to check chain convergence and parameter mixing. Maximum likelihood (ML) analyses were performed in RAXML Web-Servers (Stamatakis et al., 2008) using default parameters with 1000 bootstraps replicates.

Table 1. The sequence's accession number of the fifty species used for phylogenetic analyses

Species	Family	GenBank No.
<i>Balaenoptera musculus</i>	Balaenopteridae	NC_001601
<i>Caperea marginata</i>	Neobalaenidae	AP006475
<i>Balaena mysticetus</i>	Balaenidae	AP006472
<i>Lipotes vexillifer</i>	Lipotidae	NC_007629
<i>Physeter catodon</i>	Physeteridae	NC_002503
<i>Hippopotamus amphibius</i>	Hippopotamidae	AP003425
<i>Antilocapra americana</i>	Antilocapridae	JN632597
<i>Tragulus kanchil</i>	Tragulidae	JN632709
<i>Hyemoschus aquaticus</i>	Tragulidae	JN632650
<i>Aepyceros melampus</i>	Bovidae	JN632592
<i>Connochaetes taurinus</i>	Bovidae	JN632627
<i>Alcelaphus buselaphus</i>	Bovidae	JN632594
<i>Sylvicapra grimmia</i>	Bovidae	JN632701
<i>Philantomba monticola</i>	Bovidae	JN632687
<i>Oryx dammah</i>	Bovidae	JN632677
<i>Hippotragus equinus</i>	Bovidae	JN632647
<i>Pelea capreolus</i>	Bovidae	JN632684
<i>Kobus ellipsiprymnus</i>	Bovidae	JN632651
<i>Redunca arundinum</i>	Bovidae	JN632694
<i>Bison bonasus</i>	Bovidae	NC_014044
<i>Bos indicus</i>	Bovidae	NC_005971
<i>Bos grunniens</i>	Bovidae	NC_006380
<i>Procapra przewalskii</i>	Bovidae	NC_014875
<i>Antilope cervicapra</i>	Bovidae	NC_012098

<i>Pantholops hodgsonii</i>	Bovidae	NC_007441
<i>Ammotragus lervia</i>	Bovidae	NC_009510
<i>Ovis aries</i>	Bovidae	NC_001941
<i>Budorcas taxicolor</i>	Bovidae	NC_013069
<i>Muntiacus muntjak</i>	Cervidae	NC_004563
<i>Muntiacus crinifrons</i>	Cervidae	NC_004577
<i>Muntiacus reevesi</i>	Cervidae	NC_004069
<i>Elaphodus cephalophus</i>	Cervidae	NC_008749
<i>Cervus nippon yesoensis</i>	Cervidae	NC_006973
<i>Cervus eldi</i>	Cervidae	NC_014701
<i>Rusa unicolor swinhoei</i>	Cervidae	NC_008414
<i>Cervus elaphus yarkandensis</i>	Cervidae	NC_013840
<i>Rangifer tarandus</i>	Cervidae	NC_007703
<i>Hydropotes inermis</i>	Cervidae	EU315254
<i>Giraffa camelopardalis</i>	Giraffidae	AP003424
<i>Okapia johnstoni</i>	Giraffidae	JN632674
<i>Moschus berezovskii</i>	Moschidae	NC_012694
<i>Moschus moschiferus</i>	Moschidae	NC_013753
<i>Moschus chrysogaster</i>	Moschidae	JQ608470
<i>Sus scrofa</i>	Suidae	AJ002189
<i>Tayassu tajacu</i>	Tayassuidae	AP003427
<i>Camelus dromedarius</i>	Camelidae	NC_009849
<i>Camelus ferus</i>	Camelidae	NC_009629
<i>Lama glama</i>	Camelidae	AP003426
<i>Equus asinus</i> (out-group)	Equidae	NC_001788
<i>Equus caballus</i> (out-group)	Equidae	NC_001640

3. Results

Phylogenetic trees of Cetartiodactyla, constructed using BI and ML methods, show a similar topology (Figure 1). The initial clade in Cetartiodactyla is between Suina and Hippopotamidae/Cetaceae/Ruminantia lineages with a strongly supported rate (PP = 1.0, BS = 73) (Figure 1). Then, Tylopoda, Whippomorpha and Ruminantia form separate successive branches. All members of Ruminantia cluster together, with the Tragulidae separate from the other families. Within the Pecora, the Antilocapridae is the early offshoot, and the families Bovidae, Cervidae, Moschidae and Giraffidae were monophyletic. The Bovidae, Cervidae and Moschidae form a clade which is a sister group to the Giraffidae. Moschidae is the sister group of Bovidae, both of them form a clade which clusters with Cervidae. Our results present that the association of Hippopotamidae and Cetacea, formed Whippomorpha within Artiodactyla (PP = 1.0, BS = 100).

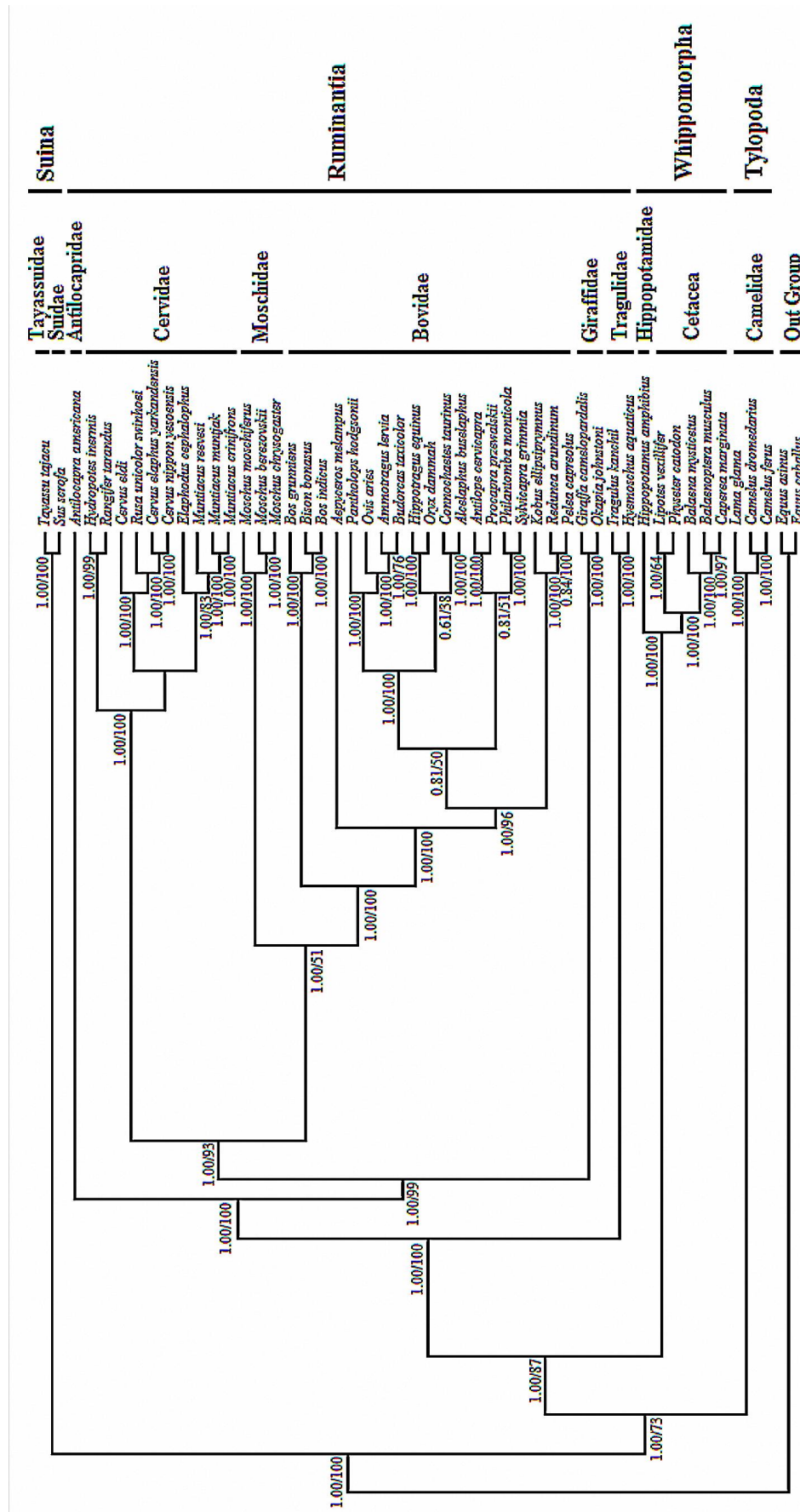


Figure 1. Molecular phylogenetic tree derived from complete DNA sequence of 12 mitochondrial protein-coding genes using Bayesian inference and ML analysis. The numbers beside the nodes are Bayesian posterior probabilities (PP) and bootstrap support (BS). *Equus asinus* and *Equus caballus* were set as out-groups

4. Discussion

During the last two decades, extensive efforts have been made to investigate phylogenetic relationships of Cetartiodactyla (e.g., O'Leary & Gatesy, 2008; Gatesy et al., 1999). However, relationships within this group remain unclear. One possibility is that different molecular marker has different evolutionary rate; even if the same maker, the substitution rate varies among taxa. Thus, a single gene or a short DNA sequence applying to phylogeny reconstruction is highly likely to produce an incorrect tree topology for a systematic bias and/or long-branch attraction (Nikaido et al., 1999). The complete mitochondrial genome provides a higher level of support for molecular systematics than those based on individual or partial mitochondrial genes (Castro & Downton, 2005; Krzywinski et al., 2006). Mitochondrial DNA, especially encoding proteins, such as 12S rDNA, 16S rDNA, Cyt b and ND4, have been frequently utilized as powerful tool for evolutionary studies of animals (Boore & Brown, 1998). In the present study, it demonstrates that the phylogenetic analyses based on complete mitochondrial genomes can well resolve the high-level relationships within Cetartiodactyla.

The issue about which taxon is basal within the Cetartiodactyla has been intensively debated and remains controversial. And three hypotheses have been proposed: Camelidae, Suidae, or Cetacea. The results of the present study are well-supported in presenting that Artiodactyla is non-monophyletic status on account of its containing Cetacea which is the sister to Hippopotamidae. These findings are also consistent with the previous studies (Murphy et al., 2001; Nikaido et al., 1999; Gatesy et al., 2002; O'Leary & Gatesy, 2008; Hassanin et al., 2012). The present study indicates that the basal divergence within Cetartiodactyla is between Suina and a strongly supported clade of the remaining Cetartiodactyla (PP = 1.0, BS = 73) (Matthee et al., 2001; Hassanin et al., 2012).

The present study unambiguously supports the basal position of the Tragulidae relative to the Pecora families with strong statistical support (PP = 1.0, BS = 100), which is consistent with the previous molecular, morphological and palaeontological evidences (Matthee et al., 2001; Price et al., 2005; Hassanin et al., 2012; Métais et al., 2007).

The position of Moschidae (musk deer) existed of disputed status within the Ruminantia. Historically, the clade has always been difficult to place. It was not until recently that Moschidae were even recognized as a separate family shifting from cervids (Corbert & Hill, 1980; Leinders & Heintz, 1980); they are now typically held to cluster with cervids and/or the bovids (Peng et al., 2009; Yang et al., 2012; Hassanin et al., 2012). Here, Moschidae is recognized as a sister group to Bovidae, and the data show Moschidae, Bovidae, Cervidae and Giraffidae to be four monophyletic groups, agreeing with the previous view that placed the Moschidae as a monophyletic family (Flerov, 1952; Janis & Scott, 1988; Li et al., 1998; Peng et al., 2009).

The molecular evidence for studies of the phylogeny in the Cetartiodactyla were restricted regarding under-representation of taxa or on the basis of partial mitochondrial sequences or on a single gene (Su et al., 2001; Matthee et al., 2001; Guha et al., 2007). Studies of this kind may sometimes deviate from the phylogenetic accuracy (Agnarsson & May-Collado, 2008), and this might lead to inconsistencies among different studies. In the present study, the amount of sequence data has provided a reasonable basis for examining the mitogenomic relationships within Cetartiodactyla. However, we are aware that though using mitogenomic datasets to reconstruct the phylogenetic tree of Cetartiodactyla acquired high support values, they can also be systematically biased (Fisher-Reid & Wiens, 2011). Therefore, to unambiguously resolve phylogenetic relationships within Cetartiodactyla, more complete mitochondrial genomes as well as multiple nuclear markers are needed for future studies.

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