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A revised phylogeny of Antilopini (Bovidae, Artiodactyla) using combined mitochondrial and nuclear genes

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ABSTRACT

Antilopini (gazelles and their allies) are one of the most diverse but phylogenetically controversial groups of bovids. Here we provide a molecular phylogeny of this poorly understood taxon using combined analyses of mitochondrial (*CYTB, COIII, 12S, 16S*) and nuclear (*KCAS, SPTBN1, PRKCI, MC1R, THYR*) genes. We explore the influence of data partitioning and different analytical methods, including Bayesian inference, maximum likelihood and maximum parsimony, on the inferred relationships within Antilopini. We achieve increased resolution and support compared to previous analyses especially in the two most problematic parts of their tree. First, taxa commonly referred to as "gazelles" are recovered as paraphyletic, as the genus *Gazella* appears more closely related to the Indian blackbuck (*Antilope cervicapra*) than to the other two gazelle genera (*Nanger* and *Eudorcas*). Second, we recovered a strongly supported sister relationship between one of the dwarf antelopes (*Ourebia*) and the Antilopini subgroup Antilopina (Saiga, Gerenuk, Springbok, Blackbuck and gazelles). The assessment of the influence of taxon sampling, outgroup rooting, and data partitioning in Bayesian analyses helps explain the contradictory results of previous studies.

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1. Introduction

Antilopini (gazelles and their allies) has been described as one of the least understood groups of bovids (Rebholz and Harley, 1999; Hernández Fernández and Vrba, 2005). The tribe Antilopini belongs to the subfamily Antilopinae, a group that also includes goats and most African antelopes (e.g., Wildebeests, Sable antelope, Duikers, Impala, Waterbucks). The sister taxon of Antilopinae is Bovinae, comprising mostly cattle and spiral-horned antelopes (e.g., Kudus). Both groups comprise the artiodactyl family Bovidae. Antilopini is a very speciose group of great biological and economic importance. The earliest fossil bovids that are clearly attributable to one of the living clades (early Middle Miocene gazelles from Fort Ternan) belong to Antilopini (Bibi et al., 2009). However, their phylogenetic relationships (e.g., if they belong to the stem- or crowngroup of Antilopini) are not known, in part because of the unresolved relationships of living antilopines themselves.

In the last decade, many researchers have worked on bovid phylogenies that included a large number of species in Antilopini (Gatesy et al., 1997; Gatesy and Arctander, 2000; Groves, 2000; Vrba and Schaller, 2000; Kuznetsova and Kholodova, 2003; Lei

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et al., 2003; Marcot, 2007; Agnarsson and May-Collado, 2008; Ropiquet et al., 2009), and a consensus has emerged on the taxonomic composition of this clade (Table 1). The most recent work by Hassanin et al. (2012) introduced new names for four subgroups of Antilopini: Antilopina, based on the genus Antilope, consists of Antilope cervicapra, Gazella spp., Nanger spp., Eudorcas spp., Antidorcas marsupialis, Ammodorcas clarkei, Litocranius walleri, and Saiga tatarica; Procaprina, based on the genus Procapra, includes the three living Procapra species; Ourebina, based on the genus Ourebia, is monotypic and includes only Ourebia ourebi; Raphicerina, based on the genus Raphicerus, includes Raphicerus spp., Dorcatragus megalotis, and Madogua spp. Historically, Ourebia and Raphicerina have been united with other small-bodied and shorthorned species, i.e., Neotragus spp. and Oreotragus oreotragus, to form the group "Neotragini". This group, however, is now known to be polyphyletic as Neotragus and Oreotragus are not closely related to Antilopini (Gentry, 1992; Matthee and Robinson, 1999; Matthee and Davis, 2001; Kuznetsova and Kholodova, 2002, 2003; Hassanin and Douzery, 1999; Marcot, 2007; Agnarsson and May-Collado, 2008; Ropiquet et al., 2009; Hassanin et al., 2012).

Within the last 6 years, three studies on Antilopini phylogenetics were published with near-complete taxon sampling at genus level based on multiple genes (Marcot, 2007; Ropiquet et al., 2009; Hassanin et al., 2012; see Fig. 1). Comparisons of these studies

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Table 1

Bovid species included in this study and their taxonomic affiliations. Species marked with an asterisk were included in the reduced-taxon set. % mol. data = percentage of available data compared to the total alignment length of 7793 nucleotides. The term "CHA-clade" is used for the taxon composed of Caprini, Hippotragini and Alcelaphini.

Subfamily	Tribe	Subtribe	Species	% mol. data
Antilopinae	Antilopini	Antilopina	Antidorcas marsupialis* Antilope cervicapra* "Cazella e l.":	97 73
			Guzellu S.I Fudorcas rufifrons	54
			F thomsoni*	90
			Gazella bennettii	54
			G. cuvieri	54
			G. dorcas*	74
			G. gazella	73
			G. leptoceros	66
			G. marica	73
			G. spekei	54
			G. subgutturosa	54
			Nanger dama*	88
			N. granti	71
			N. soemmerringi	54
			Litocranius walleri*	85
			Saiga tatarica*	81
		Ourebina	Ourebia ourebi*	79
		Procaprina	Procapra gutturosa*	73
			P. picticaudata	23
			P. przewalskii	54
		Raphicerina	Dorcatragus megalotis*	73
		*	Madoqua guentheri	25
			M. kirki*	85
			M. saltiana	73
			Raphicerus campestris*	85
			R. melanotis	63
			R. sharpei	53
	Aepycerotini		Aepyceros melampus*	92
	Alcelaphini		Damaliscus pygargus*	93
	Hippotragini		Hippotragus niger*	100
	Caprini	Caprina	Capra falconeri*	03
	Capilli	Pantholonina	Pantholons hodgsoni*	85
	Canhalanhini	i untilolophia	Subvisence minutie*	07
	Cepnalophini		Sylvicapra grimmia*	97
	Keduncini		Keaunca juivorujuia Kobus allinsinmimpus*	100
	Nootragini		Nootragus moschatus*	97
	ineotragiiii		N batesi	97 54
	Oreotragini		n. Dulesi Oreotragus oreotragus*	J4 85
				05
Bovinae	Tragelaphini		Tragelaphus imberbis*	100

reveal several parts of the tree that are debatable: within Antilopina, Antilope and the three gazelle genera Nanger, Eudorcas, and Gazella (the latter three referred to as Gazella s.l. here) always form a natural group. However, Gazella s.l. might be paraphyletic with respect to Antilope (Ropiquet et al., 2009; see also Vassart et al., 1995; Decker et al., 2009). Another disagreement is the position of Saiga as either nested within or sister species to all other Antilopina. Furthermore, the relationships of the dwarf species, especially of Ourebia, are unsettled. Ourebia was resolved as sister species to all other Antilopini (Marcot, 2007), most closely related to Antilopina (Hassanin et al., 2012), or as forming a natural group with Procapra (Ropiquet et al., 2009). The latter study also recovered Raphicerina as paraphyletic with respect to Antilopina. Finally, the genus *Procapra* was resolved as the sister group to all other Antilopini (Hassanin et al., 2012), as closely related to Raphicerina (Marcot, 2007), or as the sister taxon of Ourebia (Ropiquet et al., 2009).

Here, we aimed at improving the resolution and support of the phylogeny of Antilopini by incorporating new sequences for species that have been poorly sampled for nuclear genes, namely the genera *Antilope, Gazella, Dorcatragus,* and *Procapra.* The mitochondrial genome data set of Hassanin et al. (2012) provides a sound basis for phylogenetic studies of Artiodactyla. However, a

concatenated analysis with nuclear DNA allows for testing their phylogenetic hypotheses and might increase resolution and support. Members of all major bovid clades (Alcelaphini, Antilopini, Caprini, Cephalophini, Hippotragini, Reduncini, and Bovinae) and the genera *Aepyceros*, *Neotragus*, and *Oreotragus* were used as outgroup representatives to root the trees.

Furthermore, we aimed at understanding why previous phylogenetic analyses of Antilopini produced conflicting results (Fig. 1). We therefore compared the performance of different analytical methods, i.e., Bayesian inference, maximum likelihood and maximum parsimony, using three different taxon sets. Finally, we investigated the influence of outgroup rooting on the ingroup phylogeny of Antilopini, using a random-outgroup rooting test for Bayesian inference as well as maximum parsimony analysis.

2. Material and methods

2.1. Taxon sampling

Twenty-eight species of Antilopini form the ingroup in this analysis. Twelve species from all other major bovid groups were Download English Version:

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