



The phylogeny of Cetartiodactyla: The importance of dense taxon sampling, missing data, and the remarkable promise of cytochrome b to provide reliable species-level phylogenies

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ABSTRACT

We perform Bayesian phylogenetic analyses on cytochrome b sequences from 264 of the 290 extant cetartiodactyl mammals (whales plus even-toed ungulates) and two recently extinct species, the 'Mouse Goat' and the 'Irish Elk'. Previous primary analyses have included only a small portion of the species diversity within Cetartiodactyla, while a complete supertree analysis lacks resolution and branch lengths limiting its utility for comparative studies. The benefits of using a single-gene approach include rapid phylogenetic estimates for a large number of species. However, single-gene phylogenies often differ dramatically from studies involving multiple datasets suggesting that they often are unreliable. However, based on recovery of benchmark clades—clades supported in prior studies based on multiple independent datasets—and recovery of undisputed traditional taxonomic groups, Cytb performs extraordinarily well in resolving cetartiodactyl phylogeny when taxon sampling is dense. Missing data, however, (taxa with partial sequences) can compromise phylogenetic accuracy, suggesting a tradeoff between the benefits of adding taxa and introducing question marks. In the full data, a few species with a short sequences appear misplaced, however, sequence length alone seems a poor predictor of this phenomenon as other taxa with equally short sequences were not conspicuously misplaced. Although we recommend awaiting a better supported phylogeny based on more character data to reconsider classification and taxonomy within Cetartiodactyla, the new phylogenetic hypotheses provided here represent the currently best available tool for comparative species-level studies within this group. Cytb has been sequenced for a large percentage of mammals and appears to be a reliable phylogenetic marker as long as taxon sampling is dense. Therefore, an opportunity exists now to reconstruct detailed phylogenies of most of the major mammalian clades to rapidly provide much needed tools for species-level comparative studies.

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1. Introduction

The mammalian superorder Cetartiodactyla (whales and even-toed ungulates) contains nearly 300 species including many of immense commercial importance (cow, pig, and sheep) and of conservation interest and aesthetic value (antelopes, deer, giraffe, dol-

phins, and whales) (MacDonald, 2006). Certain members of this superorder count among the best studied organisms on earth, whether speaking morphologically, behaviorally, physiologically or genetically. Understanding the interrelationships among cetartiodactyl species, therefore, is of obvious importance.

Much of the recent phylogenetic work has focused either on higher level questions such as the placement of Cetacea with respect to Artiodactyla, and the monophyly and relationships among Cetartiodactylan suborders and families (e.g., Gatesy et al., 1999; Nikaido et al., 1999; Lum et al., 2000; Matthee et al., 2001; Murphy et al., 2001; Naylor and Adams, 2001; Thewissen et al., 2001; Hassanin and Douzery, 2003; Arnason et al., 2004; Reyes et al., 2004;

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Gu et al., 2007; Wada et al., 2007; O'Leary and Gatesy, 2008), or on lower level questions of some smaller clades within the superorder (e.g., Pitra et al., 2004; Ropiquet and Hassanin, 2004, 2005; Hassanin and Ropiquet, 2004; Willows-Munro et al., 2005; Gilbert et al., 2006; Guha et al., 2007). Hence, while a consensus seems to be emerging from a range of datasets (morphology, mitochondrial and nuclear DNA, SINEs) on many of the higher level relationships (for reviews see Price et al., 2005; Hernandez and Vrba, 2005; May-Collado and Agnarsson, 2006; O'Leary and Gatesy, 2008), understanding of species-level phylogenetics across the superorder is patchy.

Detailed species-level phylogenies are of paramount importance for comparative studies (Harvey and Pagel, 1991). In general, statistical power of comparative methods increases as taxon sampling approaches completion and as resolution increases (both adding to the number of possible sister-taxon comparisons). In addition, many methods in the toolkit of comparative biology perform best when branch length estimates are available (e.g., Felsenstein, 2004; Bollback, 2006).

To date, however, the most comprehensive primary-data-based phylogenetic study on cetartiodactylans included only 51 extant species (Gatesy et al., 2002; note that May-Collado and Agnarsson, 2006 and May-Collado et al., 2007 included 90 and 92 species, respectively, but focused on Cetacea and O'Leary and Gatesy, 2008 include 64 species but focus on extinct taxa). By combining multiple types of data for a strategically chosen set of taxa Gatesy et al. (2002) and O'Leary and Gatesy (2008) offered strong hypotheses of higher level relationships within Cetartiodactyla. However, lack of a more detailed phylogeny limits the types of questions that can be addressed using the comparative method. To remedy this Price et al. (2005), (see also Hernandez and Vrba, 2005) combined multiple phylogenetic studies, and non-quantitative taxonomies, to produce a complete phylogeny of Cetartiodactyla using a supertree approach (Bininda-Emonds and Bryant, 1998; Bininda-Emonds et al., 2002). While representing a significant advancement, the supertree has some shortcomings (for a general critique of supertree techniques see e.g. Gatesy et al., 2002). For example, large portions of the tree are simply reflecting taxonomy, rather than quantitatively addressing species interrelationships. Equally important for its use for comparative studies, the resolution of the supertree is relatively low (59.9%) and it does not provide estimates of branch lengths. A better resolved phylogeny with branch lengths, even though taxon-incomplete, may represent a more powerful tool for many comparative questions and methods.

Here, we present a near species-complete phylogeny of Cetartiodactyla based on cytochrome b sequence data. We evaluate the “reliability” of the phylogeny based on the recovery of numerous higher level benchmark clades and undisputed taxonomic groups. We argue that, at least for cytb within this group of mammals, dense taxon sampling may simultaneously overcome some of the commonly cited shortcomings of single-gene phylogenies and increase the value of the resulting phylogenies. We conclude that a profitable short-term research program will be the use of cytb data to rapidly provide species-level phylogenies for large clades across mammals providing valuable tools for comparative biology. Such phylogenies are not competing with character rich studies of relatively few taxa, nor with supertrees, but offer alternative tools, and ultimately will increase the power of supertree approaches to reconstruct even larger and better resolved “megatrees”.

2. Materials and methods

2.1. Data and phylogenetic analyses

Cytochrome data was compiled from GenBank for 276 taxa representing 266 cetartiodactylans (including two recently extinct

taxa, *Myotragus balearicus*, the ‘Mouse Goat’, and *Megaloceros giganteus*, the ‘Irish Elk’ or ‘Giant Deer’), and 10 outgroups (see Table 1 for Accession Nos.). We chose outgroup taxa representing two groups from Pegasoferae a recently proposed group hypothesized to be sister to Cetartiodactyla (Nishihara et al., 2006). Given that missing data can cause problems in phylogenetic reconstruction, we created three data matrices; one in which all taxa with available cytb sequences at least 15% of the full length (1140pb) were included (full dataset = 276 species), another set where taxa with less than 30% full sequence length were excluded (pruned dataset 1 = 249 spp) and a third one where taxa with less than 50% of the full cytb sequence length were excluded (pruned dataset 2 = 203 spp). Sequences were managed and results examined in Mesquite (Maddison and Maddison, 2007) and graphic tree files were exported from Mesquite and manipulated in Adobe Illustrator where illustrations were rendered. The sequences were aligned—a trivial task as Cytb is a protein coding gene resulting in unambiguous alignment without any gaps—using the Needleman–Wunsch algorithm in MacClade 4.07 (Maddison and Maddison, 2003). The appropriate model for the Bayesian analyses was selected with Modeltest (Posada and Crandall, 1998, 2001), using the AIC criterion (Posada and Buckley, 2004) with a parsimony tree chosen as the basis for Modeltest. The best model was GTR+ γ +I (Rodríguez et al., 1990; Yang, 1994). Bayesian analysis was performed using MrBayes V3.1.2 (Huelsenbeck and Ronquist, 2001) with settings as in May-Collado and Agnarsson (2006) with separate model estimation for first, second and third codon positions.

The Markov chain Monte Carlo search for each matrix was run with four chains for 10,000,000 generations (repeated two times), sampling the Markov chain every 1000 generations, and the sample points of the first 5,000,000 generations (pruned datasets 1–2) or 8,000,000 generations (full dataset) were discarded as “burnin”. Previously (May-Collado and Agnarsson, 2006), we showed that parsimony performed relatively poorly (in terms of recovery of benchmark clades) compared to Bayesian analyses of Cytb sequences within Cetartiodactyla. For simplicity, therefore, we here restrict our analysis to Bayesian methods.

2.2. Benchmark clades

As argued by May-Collado and Agnarsson (2006) one intuitively satisfying way to judge the reliability of phylogenetic results is the recovery of benchmark clades—clades that can be treated *a priori* as ‘known’ due to independent support from multiple lines of evidence. This can be particularly valuable when character data are relatively few, such as in single-gene analyses of many taxa, as many of the existing measures of support in one way or another scale with absolute number of characters. As Cytb is, due to high substitution rates, thought to be most reliable at lower taxonomic levels, recovering ‘known’ deeper clades gives credibility to the phylogeny as a whole.

We consider a benchmark clade ‘recovered’ in a given analysis simply if it is present in the majority rule tree from the Bayesian analysis, regardless of the posterior probability value for that clade. We are here interested in the ability of Cytb to recover clades that are undisputed. That these may in some cases be very weakly supported is unsurprising as few data are being used to resolve relationships among many taxa. Also, in the full matrix, we expect missing data to have an effect on branch support and thus note that for the few benchmark clades that are supported by values close to or lower than 50% in the full analyses, they are always more strongly supported in the pruned dataset 2, where missing data is much less of a problem.

The following clades are here treated as ‘benchmark clades’ (clade names followed by studies and types of data that have recovered them, this list of studies is meant to be representative, not exhaustive). Note that we do not wish to imply that no historical

Table 1

Species included in each analysis, and their GenBank Accession Nos

Species	Accession No.	Full 276 spp.	Pruned 1 240 spp.	Pruned 2 203 spp.
Carnivora				
<i>Canis familiares</i>	AY729880	X	X	X
<i>Panthera leo</i>	AF053052	X	X	X
Euungulata				
Order Perissodactyla				
Fam. Rhinocerotidae				
<i>Dicerorhinus sumatrensis</i>	AJ245723	X	X	X
<i>D. bicornis</i>	X56283	X	X	X
Fam. Equidae				
<i>Equus caballus</i>	AY515162	X	X	X
<i>Equus grevyi</i>	X56282	X	X	X
Fam. Tapiridae				
<i>Tapirus indicus</i>	AF145734	X	X	X
<i>Tapirus terrestris</i>	AF056030	X	X	X
Cetartiodactyla				
Sub order Tylopoda				
Fam. Camelidae				
<i>Camelus dromedarius</i>	X56281	X	X	X
<i>Camelus bactrianus</i>	EF076246	X	X	X
<i>Lama glama</i>	U06429	X	X	X
<i>Lama guanicoe</i>	Y08812	X		
<i>Lama pacos</i>	AY839860	X		
<i>Vicugna vicugna</i>	U06430	X	X	X
Sub order Suina				
Fam. Suidae				
<i>Sus barbatus</i>	Z50107	X	X	X
<i>Sus cebifrons</i>	AY920906	X	X	X
<i>Sus celebensis</i>	AY534298	X	X	X
<i>Sus philippensis</i>	AY920905	X	X	X
<i>Sus scrofa</i>	DQ315604	X		
<i>Sus verrucosus</i>	AJ314553	X	X	X
<i>Babyrousa babyrussa</i>	Z50106	X	X	X
<i>Potamochoerus larvatus</i>	AY534300	X		
<i>Potamochoerus porcus</i>	DQ315602	X	X	X
<i>Phacochoerus aethiopicus</i>	AJ314551	X	X	X
<i>Phacochoerus africanus</i>	DQ470799	X	X	
Fam. Tayassuidae				
<i>Pecari tajacu</i>	X56296	X	X	X
<i>Tayassu pecari</i>	AY534303	X	X	X
<i>Catagonus wagneri</i>	U66291	X	X	X
Sub order Ruminantia				
Fam. Tragulidae				
<i>Moschiola meminna</i>	DQ676954	X		
<i>Tragulus napu</i>	X56288	X	X	X
<i>Tragulus javanicus</i>	AB122110	X	X	X
Fam. Moschidae				
<i>Moschus berezovskii</i>	AB019640	X		
<i>Moschus chrysogaster</i>	AY684631	X		
<i>Moschus fuscus</i>	DQ417658	X	X	
<i>Moschus leucogaster</i>	AF026889	X	X	X
<i>Moschus moschiferus</i>	AY121995	X	X	X
Fam. Cervidae				
Sub Fam. Muntiacinae				
<i>Megaloceros giganteus</i>	AM182645	X	X	X
<i>Elaphodus cephalophus</i>	DQ379305	X	X	X
<i>Muntiacus crinifrons</i>	DQ445735	X	X	X
<i>Muntiacus feae</i>	AF042721	X	X	X
<i>Muntiacus muntjak</i>	DQ832255	X	X	
<i>Muntiacus reevesi</i>	AF042719	X	X	X
<i>Megamuntiacus (Muntiacus) vuquangensis</i>	AF042720	X	X	X
Sub Fam. Cervinae				
<i>Axis axis</i>	AY540851	X		
<i>Axis porcinus</i>	EF491197	X		
<i>Dama mesopotamica</i>	DQ379304	X	X	X
<i>Cervus albirostris</i>	AY044863	X	X	X
<i>Cervus dama</i>	AY397663	X	X	
<i>Cervus duvaucelii</i>	AY456908	X		
<i>Cervus eldi</i>	AY540849	X		
<i>Cervus elaphus</i>	AY397658	X	X	
<i>Cervus nippon</i>	DQ191158	X	X	
<i>Cervus schomburgki</i>	AY607036	X		X

Table 1 (continued)

Species	Accession No.	Full 276 spp.	Pruned 1 240 spp.	Pruned 2 203 spp.
<i>Cervus unicolor</i>	AY456907	X		
<i>Elaphurus davidianus</i>	AY158081	X	X	
Sub. Fam. Hydropotinae				
<i>Hydropotes inermis</i>	AJ000028	X	X	X
Sub. Fam. Capreolinae				
<i>Odocoileus hemionus</i>	X56291	X	X	X
<i>Odocoileus virginianus</i>	DQ673136	X	X	X
<i>Capreolus capreolus</i>	Y14951	X	X	X
<i>Capreolus pygargus</i>	AY820968	X	X	
<i>Alces alces</i>	M98484	X	X	X
<i>Rangifer tarandus</i>	DQ673135	X	X	
<i>Blastoceros dichotomus</i>	AY326234	X	X	
<i>Ozotoceros bezoarticus</i>	L48404	X	X	
<i>Hippocamelus antisensis</i>	DQ379307	X	X	X
<i>Mazama gouazoubira</i>	DQ379308	X	X	X
<i>Pudu puda</i>	DQ379309	X	X	X
Fam. Giraffidae				
<i>Giraffa camelopardalis</i>	X56287	X	X	X
<i>Okapia johnstoni</i>	AY121993	X	X	X
Fam. Antilocapridae				
<i>Antilocapra americana</i>	AF091629	X	X	X
Fam. Bovidae				
Sub. Fam. Bovinae		X		
<i>Myotragus balearicus</i>	AY380560	X	X	X
<i>Tetracerus quadricornis</i>	DQ984134	X		
<i>Boselaphus tragocamelus</i>	AY286441	X		
<i>Bubalus depressicornis</i>	D88642	X	X	X
<i>Bubalus bubalis</i>	EF529451	X	X	X
<i>Bubalus quarlesi</i>	D82891	X	X	X
<i>Bubalus mindorensis</i>	D82895	X	X	X
<i>Bos sauveli</i>	EF382665	X		
<i>Bos frontalis</i>	AY689187	X	X	X
<i>Bos gaurus</i>	DQ459331	X	X	X
<i>Bos grunniens</i>	DQ856609	X	X	
<i>Bos indicus</i>	DQ459332	X	X	X
<i>Bos javanicus</i>	AY689188	X	X	X
<i>Bos taurus</i>	AB090987	X	X	X
<i>Pseudoryx nghetinhensis</i>	AF091635	X		X
<i>Syncerus caffer</i>	AY534338	X	X	
<i>Bison bison</i>	AY840096	X		
<i>Bison bonasus</i>	Y15005	X	X	X
<i>Pseudonovibos spiralis</i>	AF281084	X		
<i>Tragelaphus angasii</i>	AF091633	X		X
<i>Tragelaphus buxtoni</i>	AF030263	X		
<i>Tragelaphus derbianus</i>	AF022062	X		X
<i>Tragelaphus euryceros</i>	AF036276	X	X	X
<i>Tragelaphus imberbis</i>	DQ470778	X	X	
<i>Tragelaphus oryx</i>	AF036278	X		X
<i>Tragelaphus scriptus</i>	AF036277	X		X
<i>Tragelaphus spekii</i>	AJ222680	X	X	X
<i>Tragelaphus strepsiceros</i>	AF036280	X	X	X
Sub. Fam. Cephalophinae				
<i>Cephalophus adersi</i>	AF153883	X	X	X
<i>Cephalophus callipygus</i>	AF153885	X	X	X
<i>Cephalophus dorsalis</i>	AF153884	X	X	X
<i>Cephalophus nigrifrons</i>	AF153896	X	X	
<i>Cephalophus harveyi</i>	AF153887	X	X	X
<i>Cephalophus jentinki</i>	AF153888	X	X	X
<i>Cephalophus leucogaster</i>	AF153889	X	X	X
<i>Cephalophus maxwellii</i>	AF153894	X		
<i>Cephalophus monticola</i>	AF153893	X	X	X
<i>Cephalophus natalensis</i>	AF153890	X	X	X
<i>Cephalophus niger</i>	AF153895	X	X	X
<i>Cephalophus ogilbyi</i>	AF153897	X	X	X
<i>Cephalophus rubidus</i>	AF153900	X	X	X
<i>Cephalophus rufilatus</i>	AF153901	X	X	X
<i>Cephalophus silvicultor</i>	AF153898	X	X	X
<i>Cephalophus spadix</i>	AF153899	X	X	X
<i>Cephalophus weynsi</i>	AF153902	X	X	X
<i>Cephalophus zebra</i>	AF153903	X	X	X
Sub. Fam. Hippotraginae				
<i>Redunca arundinum</i>	AF096628	X	X	X
<i>Redunca fulvorufula</i>	AF022060	X	X	X

(continued on next page)

Table 1 (continued)

Species	Accession No.	Full 276 spp.	Pruned 1 240 spp.	Pruned 2 203 spp.
<i>Redunca redunca</i>	AF096626	X	X	X
<i>Pelea capreolus</i>	AF030591	X		
<i>Kobus ellipsiprymnus</i>	DQ470800	X	X	
<i>Kobus kob</i>	AF052940	X	X	X
<i>Kobus megaceros</i>	AJ222686	X	X	X
<i>Kobus vardoni</i>	AF096630	X	X	
<i>Beatragus hunteri</i>	AF034968	X	X	
<i>Alcelaphus buselaphus</i>	AF300932	X	X	
<i>Alcelaphus (Sigmoceros) lichtensteinii</i>	AF016636/AF034967	X	X	
<i>Connochaetes gnou</i>	AF016637	X	X	
<i>Aepyceros melampus</i>	AF301739	X		
<i>Hippotragus equinus</i>	AF022060	X	X	X
<i>Hippotragus niger</i>	AF364809	X		
<i>Hippotragus leucophaeus</i>	U18274	X		
<i>Oryx beisa</i>	DQ138210	X		
<i>Oryx dammah</i>	AJ222685	X	X	X
<i>Oryx gazella</i>	AF249973	X	X	X
<i>Oryx leucoryx</i>	AF036286	X	X	X
Sub. Fam. Antilopinae				
<i>Gazella bennettii</i>	DQ919166	X		
<i>Gazella cuvieri</i>	AF030609	X		
<i>Gazella dama</i>	AF025954	X	X	X
<i>Gazella dorcas</i>	AF187709	X	X	
<i>Gazella gazella</i>	AF187697	X	X	
<i>Gazella granti</i>	AY534343	X	X	
<i>Gazella leptoceros</i>	AF187699	X	X	
<i>Gazella rufifrons</i>	AF030606	X		
<i>Gazella saudilla</i>	AF187722	X	X	
<i>Gazella soemmerringii</i>	AF030605	X		
<i>Gazella spekei</i>	AF030608	X		
<i>Gazella subgutturosa</i>	AF187718	X	X	
<i>Gazella thomsoni</i>	DQ470795	X	X	
<i>Antilope cervicapra</i>	AF022058	X	X	X
<i>Procapra gutturosa</i>	DQ001162	X	X	
<i>Procapra picticaudata</i>	EF554685		X	
<i>Antidorcas marsupialis</i>	AF036281	X	X	X
<i>Litocranius walleri</i>	AF249974	X	X	X
<i>Neotragus moschatus</i>	AF022069	X	X	
<i>Madoqua kirkii</i>	AF022070	X	X	X
<i>Madoqua guentheri</i>	AY534340	X	X	
<i>Raphicerus campestris</i>	AF030595	X		
<i>Raphicerus melanotis</i>	AF030596	X		
<i>Raphicerus sharpie</i>	AF022050	X	X	X
<i>Ourebia ourebi</i>	AF320574	X	X	X
<i>Saiga tatarica</i>	AF064487	X	X	X
<i>Oreotragus oreotragus</i>	AF036288	X	X	X
Sub. Fam. Caprinae				
<i>Capricornis crispus</i>	AB097260	X	X	X
<i>Capricornis sumatraensis</i>	EF202142	X	X	
<i>Naemorhedus caudatus</i>	AY356357	X	X	X
<i>Naemorhedus goral</i>	AY286436	X		
<i>Rupicapra rupicapra</i>	AF034725	X	X	
<i>Rupicapra pyrenaica</i>	AF034726	X	X	
<i>Oreamnos americanus</i>	D32198	X	X	
<i>Budorcas taxicolor</i>	AY669320	X	X	X
<i>Ovibos moschatus</i>	AY839564	X	X	X
<i>Hemitragus hylocrius</i>	AY846792	X	X	X
<i>Hemitragus jakari</i>	AY846791	X	X	X
<i>Hemitragus jemlahicus</i>	AF034733	X	X	
<i>Ammotragus lervia</i>	AF034731	X	X	
<i>Pseudois nayaaur</i>	AY382880	X	X	
<i>Pseudois schaeferi</i>	AF473605	X	X	
<i>Capra aegagrus</i>	DQ246788	X	X	
<i>Capra caucasica</i>	DQ246801	X	X	X
<i>Capra cylindricornis</i>	DQ246798	X	X	X
<i>Capra falconeri</i>	DQ246797	X	X	
<i>Capra hircus</i>	DQ519412	X		
<i>Capra ibex</i>	AF034735	X	X	X
<i>Capra nubiana</i>	AF034740	X	X	X
<i>Capra pyrenaica</i>	AJ010056	X	X	X
<i>Capra sibirica</i>	DQ246800	X	X	X
<i>Ovis aries</i>	AB006800	X	X	X
<i>Ovis ammon ammon</i>	AF242349	X	X	
<i>Ovis canadensis canadensis</i>	AF1121139	X	X	X
<i>Ovis dalli</i>	U17860	X	X	X
<i>Ovis nivicola</i>	AJ867264	X	X	X

Table 1 (continued)

Species	Accession No.	Full 276 spp.	Pruned 1 240 spp.	Pruned 2 203 spp.
<i>Ovis vignei</i>	AF034729	X	X	X
Sub. Fam. Panthalopinae				
<i>Pantholops hodgsoni</i>	AF034724	X	X	
Cetancodonta				
Fam. Hippopotamidae				
<i>Hippopotamus amphibius</i>	Y08813	X	X	X
<i>Hexaprotodon liberiensis</i>	Y08814	X	X	X
Cetacea (Rice, 1993)				
Sub order Mysticeti				
Fam. Balaenidae				
<i>Balaena glacialis</i>	X75587	X	X	X
<i>Balaena mysticetus</i>	U13125	X	X	X
<i>Eubalaena australis</i>	AP006473	X	X	X
<i>Eubalaena japonica</i>	AP006474	X	X	X
Fam. Balaenopteridae				
Sub. Fam. Balaenopterinae				
<i>Balaenoptera bonaerensis</i>	X75581	X	X	X
<i>Balaenoptera acutorostrata</i>	AY770548	X	X	
<i>Balaenoptera borealis</i>	X75582	X	X	X
<i>Balaenoptera edeni</i>	X75583	X	X	
<i>Balaenoptera musculus</i>	AY235202	X		X
<i>Balaenoptera physalus</i>	U13126	X	X	
<i>Balaenoptera brydei</i>	AB201259	X	X	X
<i>Balaenoptera omurai</i>	AB201257	X	X	X
Sub. Fam. Megapterinae				
<i>Megaptera novaeangliae</i>	X75584	X	X	X
Fam. Neobalaenidae				
<i>Capera marginata</i>	X75586	X	X	X
Fam. Eschrichtiidae				
<i>Eschrichtius eschrichtius</i>	X75585	X	X	X
Sub order Odontoceti				
Super Fam. Physteroidea				
Fam. Physteridae				
<i>Physeter macrocephalus (catodon)</i>	X75589	X	X	X
Fam. Kogidae				
<i>Kogia breviceps</i>	U72040	X	X	X
<i>Kogia simus</i>	AF304072	X	X	X
Super Fam. Ziphoidea				
Fam. Ziphiidae				
Sub. Fam. Ziphiinae				
<i>Ziphius cavirostris</i>	AF304075	X	X	X
<i>Berardius bairdii</i>	X92541	X	X	X
<i>Tasmacetus shepherdii</i>	AF334484	X	X	X
Sub. Fam. Hyperoodontinae				
<i>Hyperoodon planifrons</i>	AY579560	X	X	
<i>Hyperoodon ampullatus</i>	AY579558	X	X	
<i>Indopacetus pacificus</i>	AY162441	X		
<i>Mesoplodon densirostris</i>	X92536	X	X	X
<i>Mesoplodon bidens</i>	X92538	X	X	X
<i>Mesoplodon layardii</i>	AY579550	X	X	
<i>Mesoplodon mirus</i>	AY579552	X	X	
<i>Mesoplodon grayi</i>	AY579546	X	X	
<i>Mesoplodon stejnegeri</i>	AY579554	X	X	
<i>Mesoplodon ginkgodens</i>	AY579544	X	X	
<i>Mesoplodon hectori</i>	AY228109	X	X	
<i>Mesoplodon peruvianus</i>	AF492414	X	X	
<i>Mesoplodon europaeus</i>	AY579543	X	X	
<i>Mesoplodon carlhubbsi</i>	AY579539	X	X	
<i>Mesoplodon traversii</i>	AY579555	X		
Super Fam. Platanistoidea				
Fam. Platanistidae				
<i>Platanista gangetica</i>	AF304070	X	X	X
<i>Platanista minor</i>	X92543	X	X	X
Super Fam. Inoidea				
Fam. Pontoporidae				
<i>Pontoporia blainvelli</i>	AF334488	X	X	X
Fam. Iniidae				
<i>Inia geoffrensis boliviensis</i>	AF334487	X	X	X
<i>Inia geoffrensis geoffrensis</i>	AF334485	X	X	X
<i>Inia geoffrensis humboldtiana</i>	AF521110	X	X	X

(continued on next page)

Table 1 (continued)

Species	Accession No.	Full 276 spp.	Pruned 1 240 spp.	Pruned 2 203 spp.
Super Fam. Lipotoidea				
Fam. Lipotidae				
<i>Lipotes vexillifer</i>	AF304071	X	X	X
Super Fam. Delphinoidea				
Fam. Monodontidae				
<i>Delphinapterus leucas</i>	U72037	X	X	X
<i>Monodon monocerus</i>	U72038	X	X	X
Fam. Phocoenidae				
<i>Neophocaena phocaenoides</i>	AF334489	X	X	X
<i>Phocoena phocoena</i>	U72039	X	X	X
<i>Phocoena dioptrica</i>	U09681	X	X	X
<i>Phocoena sinus</i>	AF084051	X	X	X
<i>Phocoena spinipinnis</i>	U09676	X	X	X
<i>Phocoenoides dalli</i>	U09679	X	X	X
Fam. Delphinidae (Leduc et al., 1999)				
Sub. Fam. Lissodelphininae				
<i>Cephalorhynchus commersonii</i>	AF084073	X	X	X
<i>Cephalorhynchus eutropia</i>	AF084072	X	X	X
<i>Cephalorhynchus hectori</i>	AF084071	X	X	X
<i>Cephalorhynchus heavisidii</i>	AF084070	X	X	X
<i>Lagenorhynchus australis</i>	AF084069	X	X	X
<i>Lagenorhynchus cruciger</i>	AF084068	X	X	X
<i>Lagenorhynchus obliquidens</i>	AF084067	X	X	X
<i>Lagenorhynchus obscurus</i>	AY257161	X	X	X
<i>Lissodelphis borealis</i>	AF084099	X	X	X
<i>Lissodelphis peronii</i>	AF084064	X	X	X
Sub. Fam. Delphininae				
<i>Delphinus delphis</i>	AF084085	X	X	X
<i>Delphinus capensis</i>	AF084087	X	X	X
<i>Delphinus tropicalis</i>	AF084088	X	X	X
<i>Lagenodelphis hosei</i>	AF084099	X	X	X
<i>Tursiops truncatus</i>	AF084095	X	X	X
<i>Tursiops aduncus</i>	AF084091	X	X	X
<i>Stenella clymene</i>	AF084083	X	X	X
<i>Stenella coeruleoalba</i>	AF084082	X	X	X
<i>Stenella frontalis</i>	AF084090	X	X	X
<i>Stenella longirostris</i>	AF084103	X	X	X
<i>Stenella attenuata</i>	AF084096	X	X	X
<i>Sousa chinensis</i>	AF084080	X	X	X
Sub. Fam. Globicephalinae				
<i>Feresa attenuata</i>	AF084052	X	X	X
<i>Globicephala macrorhynchus</i>	AF084055	X	X	X
<i>Globicephala melas</i>	AF084056	X	X	X
<i>Grampus griseus</i>	AF084059	X	X	X
<i>Pseudorca crassidens</i>	AF084057	X	X	X
Sub. Fam. Orcininae				
<i>Orcinus orca</i>	AF084061	X	X	X
<i>Orcaella brevirostris</i>	AF084063	X	X	X
Sub. Fam. Stenoninae				
<i>Sotalia fluviatilis</i>	AF304067	X	X	X
<i>Sotalia guianensis</i>	DQ086827	X	X	X
<i>Steno bredanensis</i>	AF084077	X	X	X
<i>Incertae sedis</i>				
<i>Lagenorhynchus acutus</i>	AF084075	X	X	X

Species included in each of the analyses with respective GenBank accession numbers of cytochrome b sequences, extinct taxa are flagged with an asterisk. Classification used in the table is based on MacDonald 2006 and Rice, 1998. Note however, in some cases 'traditional' taxon membership of some families/subfamilies in MacDonald (2006) is inconsistent with recent phylogenies and in recovery of benchmark clades and in labeling clades on Figures we follow the latter when available, see text for discussion.

data have contradicted these clades, but rather that recent major studies seem to be converging on an answer, that therefore seems believable.

Cetartiodactyla—whales plus even-toed ungulates: Thewissen et al. (2001) and Boisserie et al. (2005) (morphology including fossil taxa); Arnason et al. (2002, 2004) (mitogenomic data); Matthee et al. (2001); and Murphy et al. (2001) (nuclear and mitochondrial data); Shimamura et al. (1997, 1999) (retroposon SINE data); Lum et al. 2000 (SINE data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); May-Collado and Agnarsson (2006) (cytb data); Amrine-Madsen et al. (2003) (apolipoprotein B); Corneli (2003)

(complete mitochondrial genome); Gatesy et al. (1999) (nuclear and mitochondrial data); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Tylopoda—camels, llamas, and relatives: Montgelard et al. (1997) (mitochondrial DNA); Gatesy et al. (1999) (nuclear and mitochondrial data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); Shimamura et al. 1999 (SINE data); Lum et al. 2000 (SINE data); Price et al. (2005) and Hernandez and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Ruminantia—subgroup of cetartiodactylans that digest food in two steps by regurgitating semi-digested food from the rumen: Montgelard et al. (1997) (mitochondrial DNA); Gatesy et al. (1999) (nuclear and mitochondrial data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); Price et al. (2005) and Hernandez and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies); Shimamura et al. 1999 and Lum et al. 2000 (SINE data); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Pecora—horned ruminants, all ruminants except tragulids: Janis and Scott (1987, 1988), Janis (2000), Gentry (2002), Leinders and Heintz (1980), Vislobokoda (1990) (morphological data); Montgelard et al. (1997) (mitochondrial DNA); Gatesy et al. (1999) (nuclear and mitochondrial data); Hassanin and Douzery (2003) (morphology, mitochondrial, and nuclear DNA); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); Price et al. (2005) and Hernandez and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies); Shimamura et al. 1999 and Lum et al. 2000 (SINE data). O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Bovidae—bovids, cloven-hoofed cetartiodactylans with unbranched horns (incl. cow, sheep, goat, and antelopes): Janis and Scott (1987, 1988), Janis (2000), Gentry (2002), Leinders and Heintz (1980), Vislobokoda (1990), Hassanin and Douzery (2003) (morphology, mitochondrial and nuclear DNA); Cronin et al. (1996) (K-casein gene); Cap et al. (2002) (behavioral and cytogenetic data); Price et al. (2005) and Hernandez and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies); Gatesy et al. (1999) (nuclear and mitochondrial data). O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Moschidae—musk deer: Groves et al. (1995), Janis and Scott (1987, 1988), Janis (2000), Gentry (2002), Leinders and Heintz (1980), Vislobokoda (1990) (morphological data); Hassanin and Douzery (2003) (morphology, mitochondrial and nuclear DNA); Guha et al. (2007) (16S rRNA and cytb); Cap et al. (2002) (behavioral and cytogenetic data); Price et al. (2005) and Hernandez and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies).

Cervidae—deer and muntjacs: Groves et al. (1995), Janis and Scott (1987, 1988), Janis (2000), Gentry (2002), Leinders and Heintz (1980), Vislobokoda (1990) (morphological data); Hassanin and Douzery (2003) (morphology, mitochondrial, and nuclear DNA); Pitra et al. 2004 (cytb); Randi et al. (1998) (mtDNA control region); Gilbert et al. 2006 (nuclear DNA); Guha et al. (2007) (16S rRNA and cytb); Cronin et al. (1996) (K-casein gene); Cap et al. (2002) (behavioral and cytogenetic data); Price (2005); and Hernandez and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies). O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Giraffidae—giraffe, okapi: Janis and Scott (1987, 1988), Janis (2000), Gentry (2002), Leinders and Heintz (1980), Vislobokoda (1990) (morphological data); Hassanin and Douzery (2003) (morphology, mitochondrial, and nuclear DNA); Guha et al. (2007) (16S rRNA and cytb); Cronin et al. (1996) (K-casein gene); Cap et al. (2002) (behavioral and cytogenetic data); Price (2005); and Hernandez and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies).

Antilocapridae—pronghorn (refers to evidence for placing this monotypic family outside any other family): Janis and Scott (1987, 1988), Janis (2000), Gentry (2002), Leinders and Heintz (1980), Vislobokoda (1990), Hassanin and Douzery (2003) (morphology, mitochondrial, and nuclear DNA), Cronin et al. (1996) (K-casein gene), Price et al. (2005) and Hernandez

and Vrba (2005) (from super trees based on morphological, behavioral, and molecular phylogenies).

Suina, Suidae, and Tayassuidae—pigs, warthog, peccari, javelina: Montgelard et al. (1997) (mitochondrial DNA); Gatesy 1997; Gatesy et al. 1996; Gatesy et al. (1999) (nuclear and mitochondrial data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); Montgelard et al. (1998) (combined cranioskeletal and mitochondrial DNA); Randi et al. (1996) (molecular data); Gongora and Moran (2005), Gongora et al. (2006) (mitochondrial DNA), Cronin et al. (1996) (K-casein gene), Shimamura et al. (1999), and Lum et al. (2000) (SINE data). O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Cetancodonta (Cetacea + Hippopotamidae)—toothed/baleen whales plus hippos: Geisler and Sanders (2003) and Boisserie et al. (2005) (morphology including fossils); Gatesy, 1997 and Gatesy et al. (1999) (nuclear data); Lum et al. (2000) (SINE data); Arnason et al. (2000, 2002, 2004) (mitogenomic data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); May-Collado and Agnarsson (2006) (cytb); Amrine-Madsen et al. (2003) (apolipoprotein B); Corneli (2003) (complete mitochondrial genome); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Cetacea—toothed and baleen whales: Montgelard et al. (1997) (mitochondrial DNA); Lum et al. (2000), (retropon SINE data); Shimamura et al. (1999) (SINEs); Arnason et al. (2000, 2002, 2004) (mitogenomic data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids); Messenger and McGuire (1998) (morphology); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Mysticeti—baleen whales: Arnason and Gullberg (1993) (cytb); Cassens et al. (2000) (mitochondrial DNA and proteins); Gatesy et al. (1999) and Rychel et al. (2004) (nuclear and mitochondrial data); Lum et al. (2000) (SINE data); Arnason et al. (2000, 2002, 2004) (mitogenomic data); Hamilton et al. (2001), May-Collado and Agnarsson (2006), and Yang et al. (2005) (cytb); Messenger and McGuire (1998) (morphology); Geisler and Sanders (2003) (morphology including fossils); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids); Steeman (2007) (morphological data, including fossils).

Odontoceti—toothed whales: Arnason and Gullberg (1993) (cytb); Cassens et al. (2000) (mitochondrial DNA and proteins); Lum et al. (2000), Nikaido et al. (2001, 2007) (SINE data); Arnason et al. (2000, 2002, 2004) (mitogenomic data); Hamilton et al. (2001), May-Collado and Agnarsson (2006), and Yang et al. (2005) (cytb); Messenger and McGuire (1998) (morphology); Geisler and Sanders (2003) (morphology including fossils); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Delphina (Delphinoidea plus river dolphins (minus Platanistidae))—porpoises, monodontids, and dolphins plus river dolphins other than *Platanista*. Cassens et al. (2000) (mitochondrial DNA and proteins); May-Collado and Agnarsson (2006), Yang et al. (2005), and Hamilton et al. (2001) (cytb); Arnason et al. (2004) (mitogenomic data); Messenger and McGuire (1998) and De Mui-zon (1988) (morphological data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils). O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Delphinoidea (Phocoenidae + Monodontidae + Delphinidae)—porpoises, monodontids, and dolphins: Gatesy et al. (1999) (nuclear and mitochondrial data); Cassens et al. (2000) (mitochondrial DNA and proteins); May-Collado and Agnarsson (2006) and

Hamilton et al. (2001) (cytb); Heyning (1989) (morphology); Waddell et al. (2000) (nuclear DNA); Arnason et al. (2004) (mitogenomic data); Messenger and McGuire (1998) and De Muizon, 1988 (morphology); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, mitochondrial DNA, including fossils).

Physeteroidea (Kogiidae + Physeteridae)—sperm whales: Gatesy et al. (1999) (nuclear and mitochondrial data); Cassens et al. (2000) (mitochondrial DNA and proteins); Hamilton et al. (2001), Verma et al. (2004), and May-Collado and Agnarsson (2006) (cytb); Arnason et al. (2004) (mitogenomic data); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils).

Ziphiidae—beaked whales: Gatesy et al. (1999) (nuclear and mitochondrial data); Cassens et al. (2000) (mitochondrial DNA and proteins); Hamilton et al. (2001), Verma et al. (2004), and May-Collado and Agnarsson (2006) (cytb); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); Lambert (2005) (morphological data, including fossils).

Monodontidae—monodontids, narwhal, and beluga: Cassens et al. (2000) (mitochondrial DNA and proteins); Hamilton et al. (2001), Verma et al. (2004) and May-Collado and Agnarsson (2006) (cytb); Waddell et al. (2000) (nuclear DNA); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils).

Phocoenidae—porpoises: Cassens et al. (2000) (mitochondrial DNA and proteins); Hamilton et al. (2001), Verma et al. (2004), Rosel et al. (1995), and May-Collado and Agnarsson (2006) (cytb); Fajardo-Mellor et al. (2006) (morphological data, including fossils); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils).

Delphinidae—dolphins: Cassens et al. (2000) (mitochondrial DNA and proteins); Caballero et al. (2008) (nuclear and mitochondrial DNA); Hamilton et al. (2001), LeDuc et al. (1999) and May-Collado and Agnarsson (2006) (cytb); O'Leary et al. (2004) (combined morphology, nuclear DNA, mitochondrial DNA, and amino acids, including fossils); O'Leary and Gatesy (2008) (combined morphology, nuclear DNA, and mitochondrial DNA, including fossils).

3. Results

3.1. Benchmark clades

In the full dataset, all of the benchmark clades were recovered (Figs. 1 and 2 and Table 2), except that one species *Moschiola meminna*, a member of Tragulidae grouped with Bovidae (Fig. 3), thereby rendering both families paraphyletic (according with current taxonomic classification). *Moschiola* has available sequence shorter than 30% (but slightly longer than 15%) of the full cytb sequence length is thus only included in the full matrix. In a subsequent analysis of the full matrix with this species removed the monophyly of all benchmark clades were supported (not shown). All benchmark clades were recovered in the pruned two data subset (see Table 2) and in general support was higher for many clades than in the full analysis. In the pruned 1 data subset, all benchmark clades were supported, except Odontoceti due to the placement of *Physeteroidea* whose exact placement (like in the full analysis) is particularly weakly supported.

In all the analyses, most of the currently recognized subfamilies/tribes within Cetartiodactyla were recovered as monophyletic, except subfamilies that have consistently been rejected by recent phylogenetic analyses (see Section 4). It should be noted that it can be difficult to accurately estimate agreement with taxonomy

as different authors have presented different taxonomic classifications. Our results, in general, closely resemble the most recent and most detailed phylogenetic analyses of the group, but resemble slightly less well the rather more 'traditional' classification presented in (MacDonald, 2006 see Table 1). The latter does not take into account some recent suggested changes in taxonomy based on both morphological and especially molecular data. Hence, where our results disagree with the classification presented in MacDonald (2006) the disagreement typically involves taxa whose placement has been questioned by previous phylogenetic work (e.g. *Neotragus*, *Oreotragus*, see Fig. 4) and/or monotypic subfamilies (e.g. Megapterinae, Hydroptolinae, Panthalopinae).

For clade support and detailed species-level relationships, see Fig. 5.

3.2. Higher level relationships

Our results support the following relationship among the four major cetartiodactylan lineages (((Tylopoda ((Cetancodonta (Ruminantia + Suina))), with variable support (Figs. 1, 2, and 5a and Table 2). This arrangement has not been suggested previously, to our knowledge (see review in O'Leary and Gatesy, 2008 and discussion).

Relationships among clades within Cetancodonta are identical to those found by May-Collado and Agnarsson (2006) (Figs. 2 and 5d).

Within Ruminantia all our analyses suggest the following relationships among families: (((((Tragulidae(((Antilocapridae(((Giraffidae((Cervidae(Moschidae + Bovidae))))))) with relatively high support (Figs. 1, 2, and 5a–c and Table 2), supporting the subdivision of Ruminantia into Tragulina and Pecora.

3.3. Family and subfamilies relationships

We recovered the monophyly of all families within Suina and Ruminantia in all analyses (Figs. 2 and 5a–c), with the exception noted above in the full data matrix where *Moschiola* (Tragulidae) seems misplaced within Bovidae (Figs. 2 and 5c, all Ruminantia families were monophyletic in the full matrix when this species was removed prior to analysis and the monophyly of Bovinae received much higher support, see Table 2).

Within Bovidae all analyses support Bovinae and Cephalophinae as defined by (MacDonald, 2006) (Figs. 2 and 5a–c). All analyses also support slightly modified Caprinae and Antelopinae, (see Table 2 and Section 4). All analyses support the groups Reduncini, Hippotragini, and Alcelaphini, variously treated as tribes (e.g. by MacDonald, 2006) or subfamilies (Figs. 2 and 5a–c). However, our results conclusively reject Hippotraginae sensu MacDonald (2006) that groups these three. Our results are also consistent with the monotypic subfamilies Aepycerotinae (Impala, *Aepyceros melampus*) and Peleinae (Grey Rhebok, *Pelea capreolus*) as these do not nest within other subfamilies, but not with the monotypic Panthalopinae (Tibetan antelope, *Pantholops hodgsonii*) which nests within Caprinae (Figs. 2 and 5a–b). Within Bovidae the following relationship between subfamilies is supported by the three analyses ((((((Bovinae (((((Aepycerotinae (((((Reduncinae + Peleinae) (((Cephalopinae + Antelopinae) (Caprinae (Hippotraginae + Alcelaphinae))))))))))))) (Fig. 3). Our results support prior findings (e.g. Matthee and Davis, 2001) that *Neotragus moschatus* (Suni Antelope) does not belong to Antelopinae. In the full dataset analyses *Neotragus* groups with Aepycerotinae (Impala) but with weak support (Figs. 2 and 5b). Our results also reject the inclusion of *Oreotragus* (Klipspringer) in Antelopinae (Figs. 2 and 5b), which rather may belong to Cephalophinae where it groups with strong support in all analyses and with which it shares striking morphological similarities (Fig. 4).

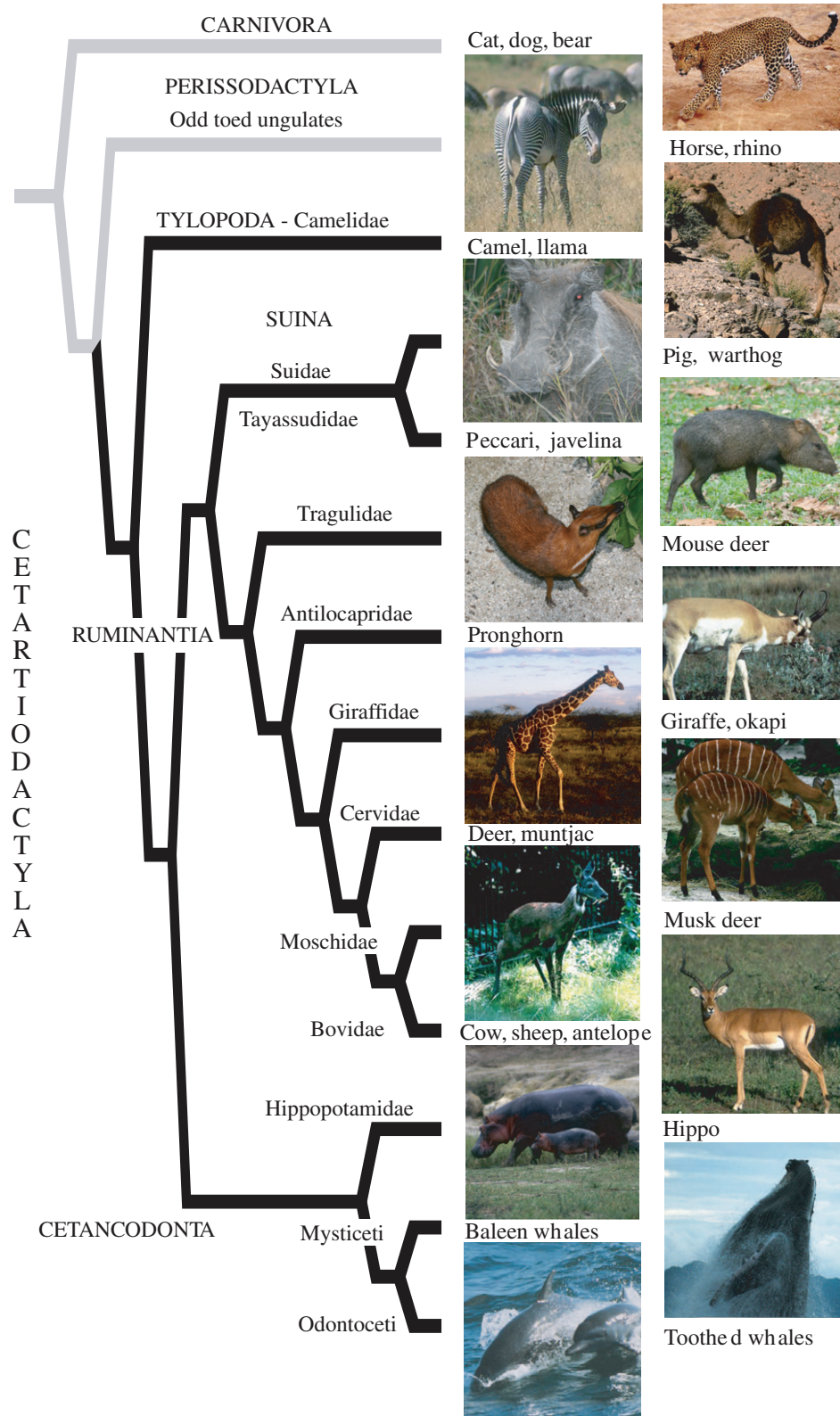


Fig. 1. Summary cladogram of the full analyses showing higher level relationships among major clades within Cetartiodactyla. Photos by I. Agnarsson and L. May-Collado, except: warthog and mouse deer provided by M. Kuntner, peccary by M. Saborio, and musk deer (copyright K. Kutundisz) and pronghorn (copyright J.O. Wolff) obtained with permission from the ASM Mammal Image Library.

In the pruned datasets 1 and 2, our results support the monophyly of the five major groups (treated variously as subfamilies or tribes) within Cervidae (Figs. 3 and 5b): Cervinae (including the extinct *Megaloceros* ‘Giant deer’), Odocoileinae, Muntiacinae,

Capreolinae, and Alceinae (see Gilbert et al., 2006 where these are treated as tribes). However, our results differ from those of Gilbert et al. (2006) in the interrelationships of these groups. We find that Capreolinae and Alceinae are sister and together

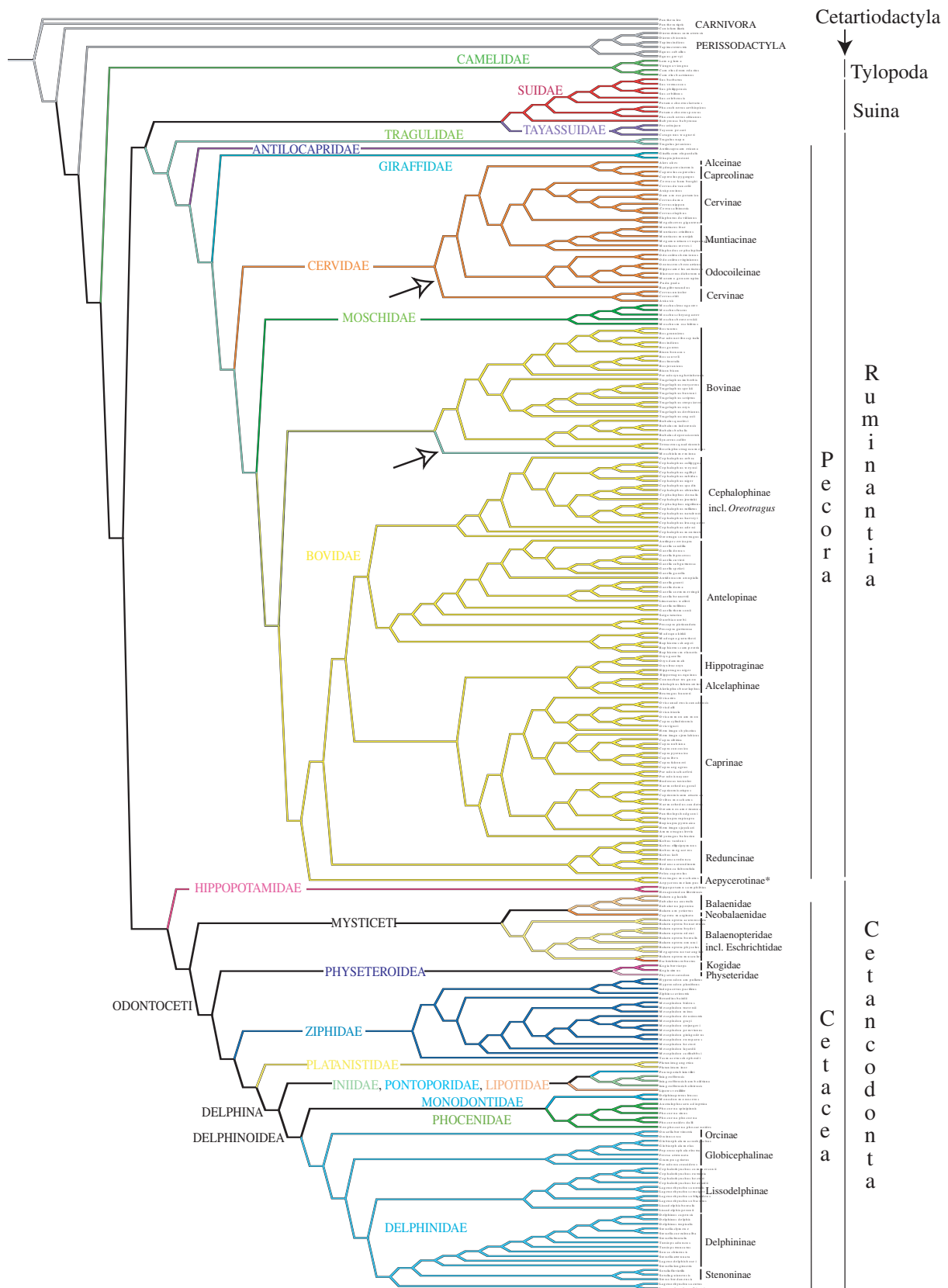


Fig. 2. Majority rule consensus of the Bayesian analyses of the full dataset. Cladogram is colored according with families, labels include all benchmark clades and major groups at the level of subfamily and above. Subfamilies whose monophyly has been consistently rejected by prior phylogenetic analyses (e.g. ziphiid subfamilies) are omitted. Arrows indicate species that appear misplaced given current knowledge. At the family level this includes only the tragulid *Moschiola meminna* that groups within Bovidae. At the subfamily level, this includes a clade of three Southeast Asian Cervinae species placed sister to the remaining Cervidae and apart from other cervines.

Table 2

Recovery and support of benchmark clades and subfamilies within Cetartiodactyla. Numbers are posterior probability values

Benchmark clades	Full matrix	Pruned matrix 1	Pruned matrix 2
Cetartiodactyla	50	100	99
Tylopoda	98	100	100
Ruminantia	60	100	100
Pecora	60	100	100
Bovidae	NO/41 ^j	65	80
Moschidae	100	100	100
Cervidae	100	100	100
Giraffidae	64	60	64
Antilocapridae ^a	60	83	98
Suina	100	100	100
Suidae	100	100	100
Tayassuidae	100	100	100
Cetancodonta	99	100	100
Cetacea	100	100	100
Mysticeti	100	100	100
Odontoceti	27	NO	84
Delphina	100	100	100
Delphinoidea	86	41	70
Physeteroidea	99	90	88
Ziphiidae	100	100	100
Monodontidae	100	100	100
Phocoenidae	100	100	100
Delphinidae	100	100	100
Subfamilies			
Odocoileinae ^b	100	100	100
Capreolinae	100	100	100
Hydropodinae ^c	100	100	100
Cervinae	NO	88	100
Muntiacinae	99	100	100
Bovinae	49	100	100
Reduncinae/Reduncinae incl. Peleaeinae	72/95	86	100
Antelopinae/sans Neotragus and Oreotragus ^d	NO/100	NO/100	NO/100
Hippotraginae sensu MacDonald/Hippotraginae ^e	NO/99	NO/100	NO/100
Alcelaphinae (Alcelaphini)	56	100	100
Cephalophinae	100	100	100
Caprinae ^f	100	100	100
Balaenopterinae/sensu lato ^g	NO/100	NO/100	NO/100
*Megapterinae ^h	NO	NO	NO
*Ziphiinae	NO	NO	NO
*Hyperodontinae	NO	NO	NO
Lissodelphininae ⁱ	100	100	100
Delphininae	100	92	100
Globicephalinae	100	100	100
Orcininae	95	91	92
Stenoninae	69	70	87

Recovery of Benchmark clades and subfamilies in the three matrices. Full matrix (including all species with at least 15% of full length cytb sequence available), pruned matrix 1 (species with 30% or more of full sequence length), and pruned matrix 2 (species with 50% or more of full sequence length). Classification follows MacDonald (2006) and/or recent phylogenetic studies as discussed in text. Subfamilies marked with an asterisk are ones that have been consistently rejected by prior phylogenetic work and whose rejection here thus indicates signal congruent with other data.

^a Represented by a single species, number refers to support for its placement outside any other family.

^b Odocoileini sensu Gilbert et al. (2006).

^c This monotypic subfamily in all analyses nests sister to the remaining Capreolinae with strong support, consistent with either its inclusion in Capreolinae or its redundant placement in its own family, see also Gilbert et al. (2006).

^d Previous studies have questioned the placement of *Neotragus* and *Oreotragus* in Antelopinae (e.g. Matthee and Davis, 2001 based on nuclear and mitochondrial DNA), see text for discussion.

^e Hippotraginae sensu (MacDonald, 2006) includes the tribes Reduncini, Alcelaphini, and Hippotragini, whereas some other authors treat these three groups as separate subfamilies, in all our analyses the three are tribes are monophyletic, but Reduncini never clusters with the other two. This finding supports the latter view of treating the three as subfamilies.

^f Caprinae is here treated as including *Pantholops hodgsoni*, traditionally in Antelopinae or its own subfamily Pantholopinae (see MacDonald, 2006), however, multiple studies based on both morphology and molecular data have shown that this species, the "Tibetan antelope", is in fact, a goat (Gentry 2002). Caprinae also includes the extinct Balearic Island Cave Goat (*Myotragus balearicus*).

^g The monophyly of Balaeopteridae has been refuted numerous times based on molecular data, the monotypic family Eschrichtiidae always nests within it. Based on these results both *Eschrichtius eschrichtius*, and *Megaptera novaeangliae* should be placed in the genus *Balaenoptera*, hence within Balaeopterinae (also rejecting the subfamily Megapterinae).

^h See footnote g, this monotypic subfamily in most studies nests within the genus *Balaenoptera*.

ⁱ Sensu May-Collado and Agnarsson (2006) and excluding *Lagenorhynchus acutus* and *L. albirostris*, treated by MacDonald (2006) as incertae sedis.

^j *Moschiola meminna* (Tragulidae) here nests within Bovidae rendering both families paraphyletic, see text. Support value after "/" refers to Bovidae including *Moschiola*.

more closely related to Muntiacinae + Cervinae than to Odocoileinae.

There is additional conflict in the full dataset, where three supposedly Cervinae species, the Southeast Asian *Cervus unicolor*, *Cervus eldi*, and *Axis axis*, group sister to the remaining Cervidae

rendering Cervinae (and Plesiometacarpalia) paraphyletic (Fig. 2). This arrangement appears well supported in our analyses, but contradicts prior phylogenies and may be due to the fact that the three all have short sequences and are thus only present in the full dataset.

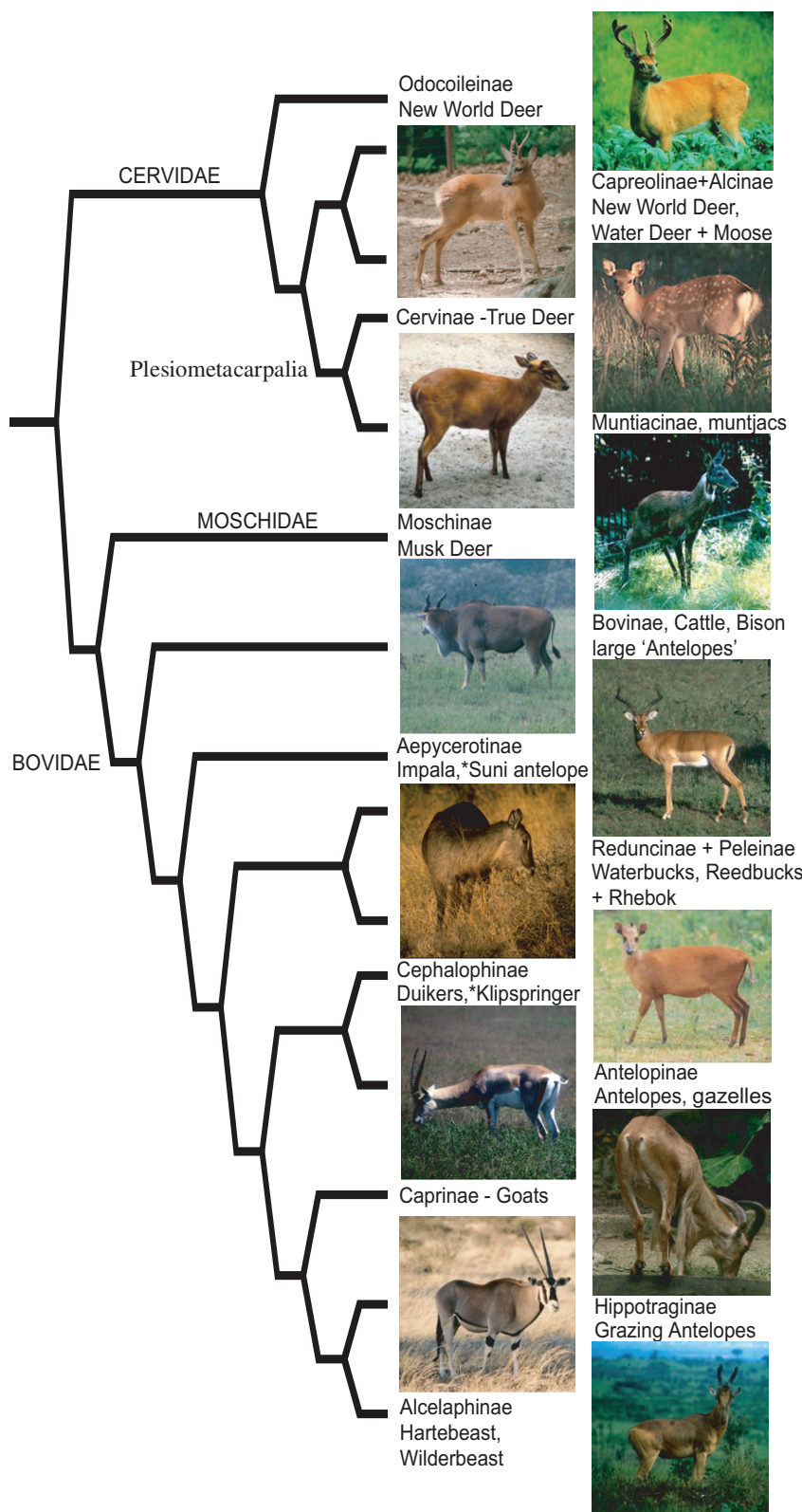


Fig. 3. Summary cladogram of Bovidae, Cervidae and Moschidae. Photos by I. Agnarsson and L. May-Collado, except: *Capreolus capreolus* copyright Ralf Schmode; and *Sylvicapra grimmia* copyright G.C. Hickman, and *Moschus moschiferus* copyright K. Kutunidis, the latter two obtained with permission from the ASM Mammal Image Library.

Within cetaceans, with the exception of Balaenopteridae and Eschrichtidae (which have consistently been rejected, see e.g. May-Collado and Agnarsson, 2006 and Discussion), all families within Cetacea were recovered (Figs. 2 and 5d). At the level of sub-

families the picture is more complex. As we and others have found previously (e.g. May-Collado and Agnarsson, 2006), molecular data continues to reject the monophyly of the subfamilies within Ziphiidae (Ziphiinae = *Ziphius*, *Tasmacetus*, and *Berardius*, Hyper-



Fig. 4. The Klipspringer (*Oreotragus*) (left) traditionally is placed within Antilopinae, but shares striking similarities with the Duikers (Cephalophinae) (right) where it groups with strong support in all our analysis. Photo of Klipspringer provided by S. Barrett, that of the duiker obtained from the Karee Safari website: <http://www.kareesafaris.co.za>.

oodontidae = *Hyperoodon*, *Mesoplodon*, and *Indopacetus*) and within Phocoenidea (Phocoeninae and Phocoenoidinae). Within Delphinidae we recover all subfamilies except Delphininae (Figs. 2 and 5d) due to the placement of *Lagenorhynchus* (as found previously by LeDuc et al., 1999, and May-Collado and Agnarsson, 2006). Our full analysis suggests the following subfamilies relationships: (((Orcinae (((Globicephalinae ((Lissodelphininae (Stenoninae + Delphininae)))). However, this arrangement had very weak support (Fig. 2) and the phylogenetic relationships between subfamilies were not consistent between analyses (Fig. 5d). Our results continue to reject current taxonomic classification with regards to *Lagenorhynchus* (May-Collado and Agnarsson, 2006).

3.4. Extinct species

The extinct ‘mouse goat’ (*M. balearicus*) did not group with goats, but rather as sister to remaining Caprinae, the clade containing goats, sheep, and relatives. Lalueza-Fox et al. (2005) similarly refuted the placement of *Myotragus* among goats, but in their analysis it grouped sister to sheep. The extinct ‘Irish Elk’ (*M. giganteus*) is here within Cervinae sister to Père David’s Deer (*Elaphurus davidianus*) and together these group with fallow deer (*Dama*).

4. Discussion

4.1. Recovery of benchmark clades: the reliability of cytochrome b and importance of dense taxon sampling

Nearly all benchmark clades were recovered in all analyses (Figs. 1–3 and 5 and Table 2). At the level of families the only real inconsistency surrounds a single species with a very short sequences available (*Moschiola*, Fig. 2). Otherwise, our results differ only from some traditional classifications in the placement of species whose phylogenetic position has been questioned by many previous studies (i.e. taxa that recent evidence suggests are misplaced in traditional classifications). Furthermore, our results, as far as comparable, are identical to the most character-complete analysis of extant Cetartiodactyla to date, scoring 28 taxa for a massive dataset of over 600 morphological and 40,000 molecular characters (O’Leary and Gatesy, 2008, their Fig. 7, but note that the inclusion of fossils impacted their results and their total evidence tree differs slightly in the placement of Suina and Moschiidae). This is a remarkable result for several reasons. First, single-gene analyses rarely give results that agree with global optima. Second, the ratio of character data to number of taxa is relatively low so that cytb seems to contain

remarkable level of information at various phylogenetic levels. In fact, cytb has been used successfully for phylogenetic analyses of populations within species (Ludt et al., 2004), yet it resolves divergences as old as 60 million years (see e.g. O’Leary and Gatesy, 2008) or more. Third, previous studies involving two to many genes often fail to recover ‘known’ clades within Cetartiodactyla, including previous analyses using cytb. The latter implies that sparse taxon sampling in previous studies is, at least partially, to blame.

We provide two examples to show evidence that dense taxon sampling increases phylogenetic accuracy with the cytb gene. Guha et al. (2007) analyzed relationships within the infraorder Pecora using many fewer taxa than included here, but using an additional loci, 16S. They found that “Consistent with the findings of most previous molecular investigations, we could not unambiguously resolve the monophyly of Bovidae... This apparent paraphyly of Bovidae may be attributed to the distant position of the Tragulidae outgroup and the subsequent saturation of substitutions in the Pecora/Tragulina comparisons. In an evolutionary context, the rapid cladogenesis of Bovidae offered little time for mutations to accumulate along common stems, thereby complicating the molecular analysis. Future work with additional data and more taxa will be required to unambiguously resolve the monophyly of Bovidae” (Guha et al. 2007, p. 593). Similarly Wada et al. (2007) analyzed a small set of taxa and emphasized that cytb failed to recover the monophyly of Bovidae, while analysis of 13 mitochondrial genes did recover it. In contrast, our study with much denser taxon sampling, even though based on a single gene, recovers the monophyly of Bovidae (apart from the wayward *Moschiola* in the full analysis, see below) and every subfamily within it (Figs. 2 and 5a–c). For another example O’Leary and Gatesy (2008) discuss how their finding differs from several previous studies in the placement of Camelidae as sister to the remaining Cetartiodactyla. They suggest that the more distal placement of Camelidae in previous studies “...apparently was driven by the extensive mitochondrial genome data...in these combined matrices... but the larger sampling of nuclear loci in the present study overturned the mitochondrial genome data and supported a basal positioning of Camelidae within Cetartiodactyla”. However, our study, even though based only on a single mitochondrial gene, also supports Camelidae + remaining Cetartiodactyla (Fig. 1); hence it may not be that the mitochondrial data were misleading in previous studies, but rather that dense taxon sampling just like adding character data increases phylogenetic accuracy (e.g., Graybeal, 1998; Hillis, 1996, 1998; Hillis et al., 2003; Pollock et al., 2002; Zwickl and Hillis, 2002; contra e.g. Rokas and Carroll 2005).

In the rare cases where our results are inconsistent with benchmark clades, ad hoc explanations seem reasonable. The placement of *M. meminna* (Tragulidae) within Bovidae is likely an artifact of missing data, although remarkably it is the only conspicuous misplacement of a species across the whole phylogeny at the family level (while three species appear to be misplaced at the subfamily level within Cervidae in the full analysis, see Fig. 5a). This is supported by the fact that the placement of *Moschiola* receives low support, and the removal of *Moschiola* prior to analysis increases dramatically the support for clades close to where it nested (not shown, analysis available from authors), suggesting it had a tendency to ‘jump around’. Two other possibilities cannot be ruled out, however. One, that possibly the available sequence in Genbank may be mislabeled. And second, it should be kept in mind that the validity of Tragulidae has never been tested with molecular data including more than two species (see e.g. Price et al., 2005). Hence, it seems too early to rule out the possibility that it is not monophyletic. That the

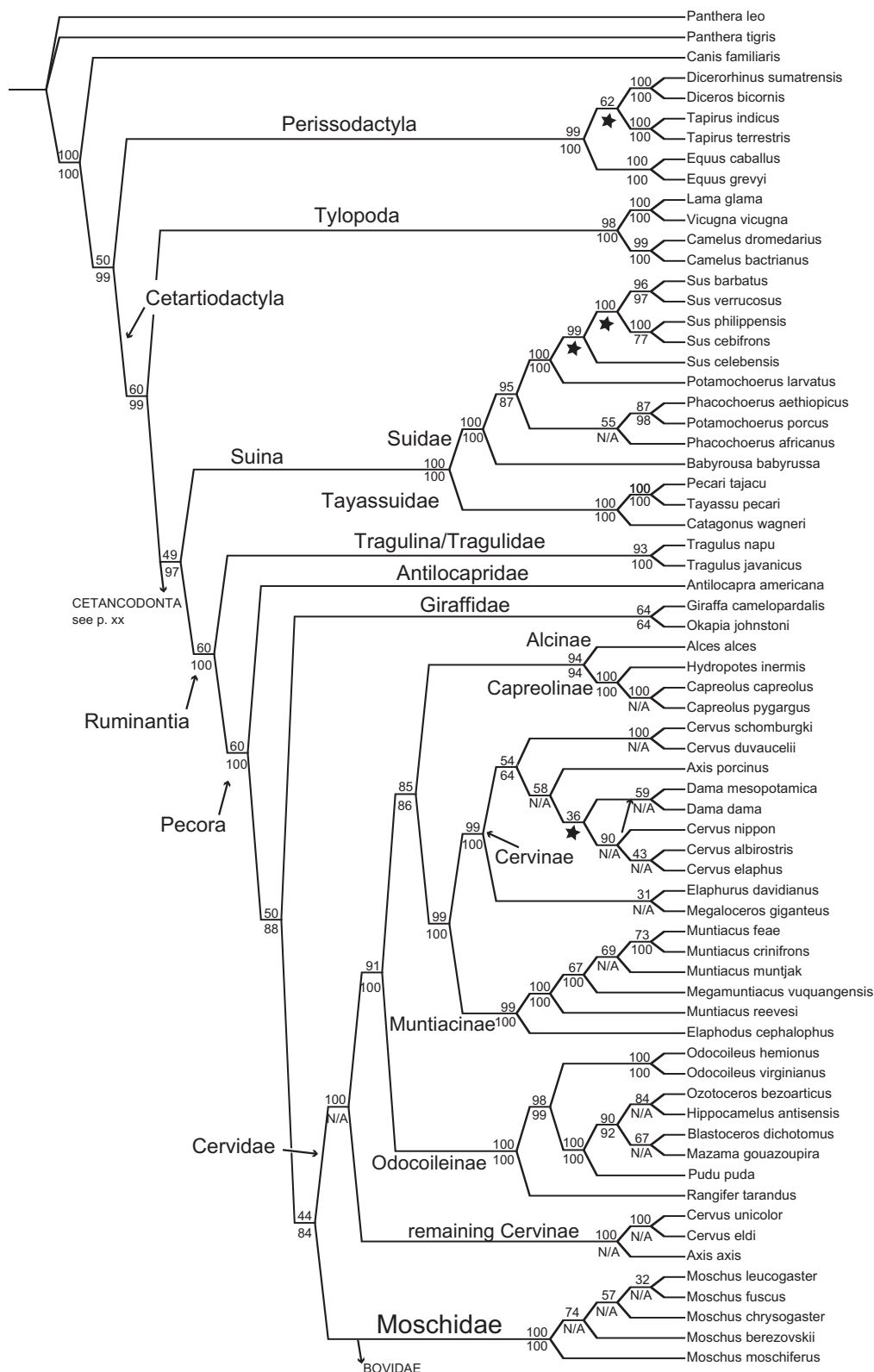


Fig. 5. Majority rule consensus of the Bayesian analyses of the full dataset with major clades labeled. Values above branches show posterior probabilities in the full analysis, below branches posterior probabilities of the analysis of the pruned dataset 2. Clades that are not tested in the pruned dataset 2 (due to absence of species in the analysis) are labeled "N/A", clades recovered in the full analysis but rejected in the pruned dataset 2 analysis are marked with a star. (a) Outgroups, Tylopoda, Suina, and Ruminantia minus Bovidae. (b) Bovidae, minus Bovinae. (c) Bovinae plus *Moschiola* (Tragulidae). Note that when *Moschiola* is removed prior to analysis (see Section 4) the support for Bovinae in the full dataset increases dramatically to 97. (d) Cetancodontia.

sequence of *Moschiola* is conspicuously different from the two other tragulids here included (personal observation) is consistent with either of these two possibilities.

The non-monophyly of Odontoceti in the pruned dataset 1 is unsurprising. There is a long history of failure to recover Odontoceti with mitochondrial data, presumably because an explosive

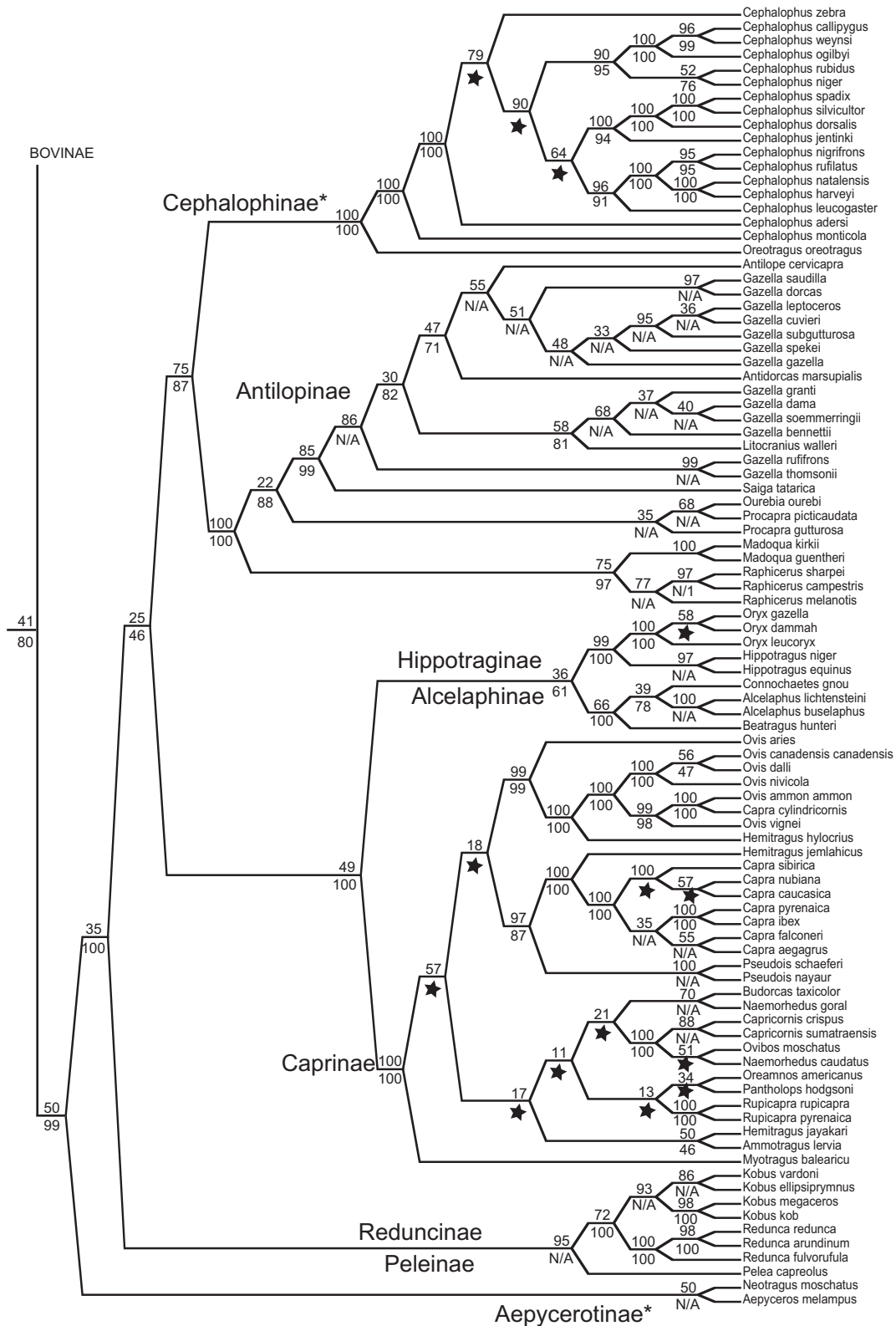


Fig. 5 (continued)

radiation took place early in the evolutionary history of whales, with little time to accumulate synapomorphies for major lineages such as Odontoceti (Arnason et al. 2004). However, with large enough character data sets (entire mitochondrial genome, Arnason et al. 2004), or dense taxon sampling (May-Collado and Agnarsson 2006) Odontoceti has been supported by mitochondrial data. Here,

we find that Odontoceti is recovered when missing data is minimized (pruned dataset 2) and when taxon sampling is most dense (full dataset, although there is essentially equal support for the placement of Physteroidae within, or outside, Odontoceti). This suggests a complicated relationship between the benefits of adding taxa versus the problems with missing data (i.e. adding taxa with

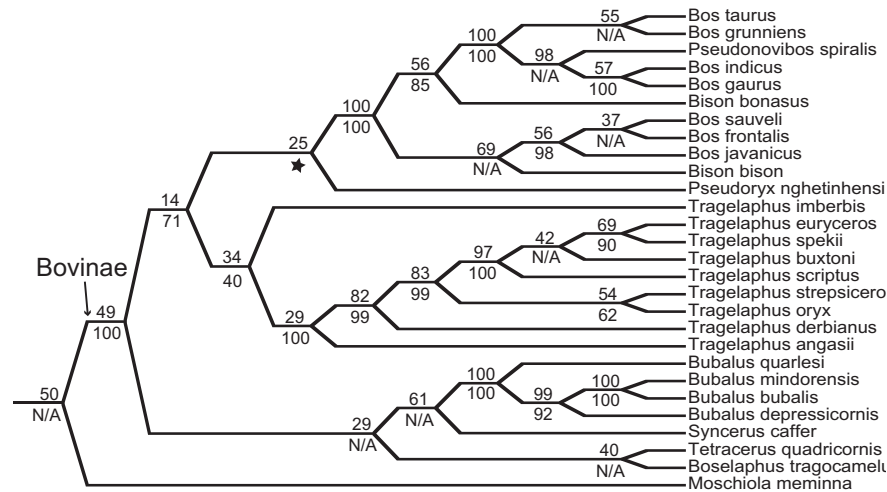


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partial sequences). The generally higher support values for clades in the pruned datasets 1 and 2 than in the full dataset similarly suggest a complex relationship. Broadly it seems that clades supported by values of 25 or above in the full analysis tend to be recovered with higher support (often much higher) in the pruned analyses, while clades supported by values of 20 or less in the full analyses are typically contradicted by the pruned analyses (Fig. 5). In general, we find that adding taxa with incomplete sequences appears rarely misleading in our analysis (as few clades are contradictory between the full and the pruned datasets), but often results in lowered support values.

Our findings suggest that *cytb* contains a remarkable amount of phylogenetic information at various taxonomic levels. They also serve to remind us that just like adding characters adding taxa adds *data* (e.g. Miller and Hormiga, 2004; Geuten et al. 2007). While character rich (but typically relatively taxon poor) studies such as the one of O'Leary and Gatesy (2008) may be better suited to address high-level relationships than an analysis such as ours (e.g. Rokas and Carroll 2005), poor taxon sampling can also be problematic (e.g., Naylor and Brown, 1998; Soltis et al., 2004; Philippe et al., 2005; Hedtke et al., 2006) and thus densely sampling taxa may be just as important for phylogenetic accuracy (e.g., Graybeal, 1998; Hillis, 1996, 1998; Hillis et al., 2003; Pollock et al., 2002; Zwickl and Hillis, 2002). And, as a beneficial side effect, dense taxon sampling also results in phylogenies with a broader general utility than taxon-sparse analyses.

4.2. Higher level relationships

In terms of higher level relationships, our findings in many cases agree with recent studies based on more character data but sparser taxon sample (Figs. 1, 2, and 5). This is particularly true for relationships that have been relatively stable in previous analyses and for comparisons with studies using SINE's, multiple genes, and/or genes plus morphology. However, for relationships among groups that have been much disputed, our findings are most similar to the most character-complete study of Cetartiodactyla to date, that of O'Leary and Gatesy (2008). Previous studies disagree on the relationships among the four major cetartiodactylan lineages, often finding low support for any given arrangement (e.g. Ursing et al., 2000). Perhaps the most frequently suggested arrangement is (((Tylopoda ((Suina (Cetancodonta + Ruminantia)))) (e.g. Boissarie et al., 2005; Price et al., 2005; O'Leary and Gatesy,

2008), while Arnason et al. (2002) and O'Leary et al. (2004) suggested ((Suina + Tylopoda) (Cetancodonta + Ruminantia)), and Ursing et al. (2000) proposed (((Suina ((Tylopoda (Cetancodonta + Ruminantia)))) among others. Our results suggest (((Tylopoda ((Cetancodonta (Ruminantia + Suina)))) (see Figs. 1 and 2) which differs from O'Leary and Gatesy (2008) only in the placement of Suina with Ruminantia, instead of sister to Ruminantia plus Cetancodonta. However, in their study, the placement of Suina was unresolved in the strict consensus suggesting we must still conclude that the relationship among these groups, or minimally the placement of Suina, is still an open question.

Relationships among clades within Cetancodonta are better agreed upon in general and, unsurprisingly, our results are near identical to those found by our previous analyses of that clade (see May-Collado and Agnarsson, 2006 for discussion).

Within Ruminantia all our results support its subdivision into Tragulina and Pecora and suggest the following relationships among families: (((((Tragulidae(((Antilocapridae(((Giraffidae ((Cervidae(Moschidae + Bovidae)))))) (see Figs. 1, 2, and 5). The relationship of these large groups has been unstable in previous studies (for reviews see Hassanin and Douzery, 2003 and Price et al., 2005; see also Beintema et al., 2003; Mahon, 2004; Guha et al., 2007; O'Leary and Gatesy, 2008). For example, Hassanin and Douzery (2003) analyzed seven loci including both mitochondrial and nuclear data their parsimony analysis supported the same relationships as we present here. However, they did not find conclusive support for the relative position of Antilocapridae and Giraffidae and hence they left these unresolved in their preferred hypothesis as sister to ((Cervidae (Moschidae + Bovidae)). In all our analyses, however, the placement of Antilocapridae as sister to the remaining Pecora is well supported (Fig. 5a, the same arrangement was found by Kuznetsova et al., 2002, although their analysis did not include Moschidae). Similarly, O'Leary and Gatesy (2008) did not conclusively resolve the relationships among these groups. Interestingly, our results are identical to their analysis of extant taxa based on extensive molecular and morphological character data (their Fig. 7). However, their combined extant and extinct data placed Moschidae as sister to the remaining Pecora representing "a rare case where inclusion of fossils overturned relationships supported by an extensive sample of molecular and morphological data for extant species". Given that his arrangement was supported by a minimal Bremer support of 1 (O'Leary and Gatesy, 2008, Fig. 4), further work is needed to examine why the inclusion of fossil taxa has this effect on the placement of Moschidae.

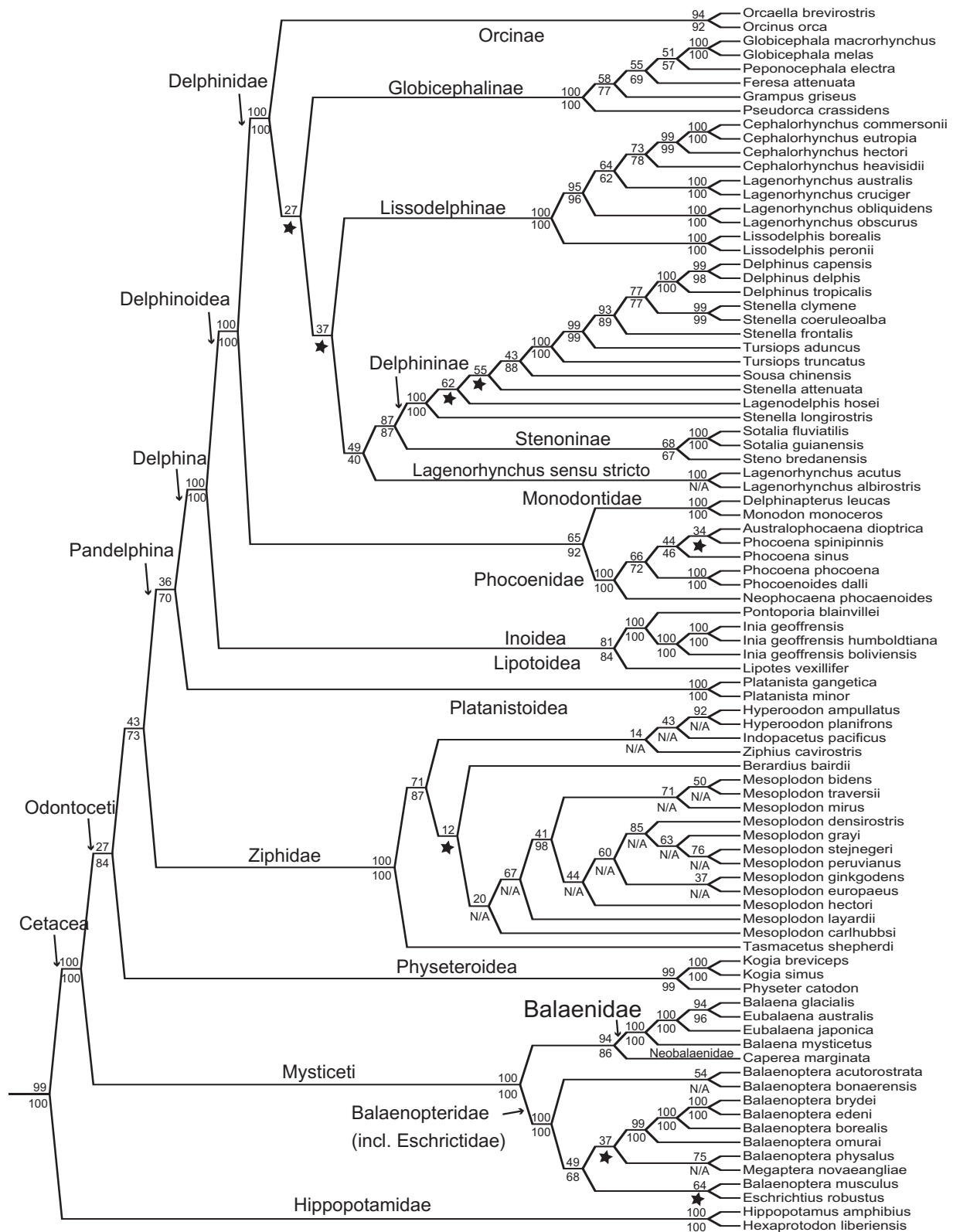


Fig. 5 (continued)

4.3. Family and subfamily relationships

It is more complicated to estimate the agreement of our results with existing taxonomy at the levels of subfamilies and tribes both because different authors propose conflicting taxonomic hypotheses that often coexist in literature, and sufficiently detailed spe-

cies-level phylogenies have often previously been lacking to choose among these hypotheses. The extensive use of detailed ranks also confuses (e.g. Kuntner and Agnarsson, 2006), and the same clades are treated as different ranks by different authors. However, our findings generally agree well with the best available recent low-level phylogenies.

Within Bovidae all analyses support Bovinae and Cephalophinae as defined by (MacDonald, 2006) (Figs. 3 and 5b–c). All analyses also support slightly modified Caprinae and Antelopinae (Fig. 5b), following strong evidence from previous studies that was not incorporated by MacDonald (2006, see e.g. Matthee and Davis, 2001; Hassanin and Douzery, 2003). All analyses support the groups Reduncini, Hippotragini and Alcelaphini, variously treated as tribes (e.g. by MacDonald, 2006) or subfamilies. However, our results conclusively reject Hippotraginae sensu MacDonald (2006) that groups these three (Figs. 2, 5b), as have other studies (e.g. Matthee and Davis, 2001; Hassanin and Douzery, 2003). Within Bovidae the following relationship between subfamilies is supported by the three analyses (((Bovinae (((Reduncinae (((Cephalopinae + Antilopinae) (Caprinae (Hippotraginae + Alcelaphinae))))))))) (Fig. 3). This arrangement is consistent with the phylogeny of Hassanin and Douzery (2003) but better resolved. Our results support prior findings that *Neotragus* does not belong to Antelopinae (e.g. Matthee and Davis, 2001), and according with our results it could possibly belong to Aepycerotinae (with the Impala) (see Figs. 2 and 3), however, support is weak for its placement and further analyses are necessary to clarify its phylogenetic placement. Our results also reject the inclusion of *Oreotragus* (Klipspringer) in Antelopinae, but rather may belong to Cephalophinae (Duikers). In light of this result, it is worth noting the striking similarities between the Klipspringer and the Duikers (Fig. 4).

Within Cervidae there is, similarly, little stability in the taxonomic categories (both ranks and membership of taxa) used by different authors. MacDonald (2006) includes the subfamilies Muntiacinae, Cervinae, Capreolinae, and the monotypic Hydropotinae, while Gilbert et al. (2006), in a recent detailed phylogeny using multiple genes, divided the family into two subfamilies (Cervinae containing two tribes Cervini and Muntiacini, a group also termed “Plesiometa-*carpalia*”) and Capreolinae containing three tribes Odocoileini, Capreolini and Alceini (a group also termed “Telemeta-*carpalia*”). Our results are more consistent with Gilbert et al. (2006) and we will compare our results to their taxonomic groups, although for consistency we will discuss their five tribes as subfamilies. In the pruned datasets 1 and 2 our results support the monophyly of all six subfamilies: Cervinae, Odocoileinae, Muntiacinae, Hydropotinae, Capreolinae, and Alceinae. However, the relationships among these groups differ in our study from those found by Gilbert et al. (2006) in that Capreolinae and Alceinae are sister and together more closely related to muntiacinae + Cervinae than to Odocoileinae. Hence, our results are inconsistent with Telemeta-*carpalia*, but still support Plesiometa-*carpalia*. It should be noted that these two groups were originally proposed based on a single character (defining one group by the plesiomorphic and the other by the derived character state), an approach that has historically, and unsurprisingly, often resulted in paraphyletic taxonomic groups. Despite its name, the Plesiometa-*carpalia* condition, the presence of only the proximal part of the lateral metacarpals, is the derived one (see e.g. Gilbert et al., 2006) and our results from the pruned analyses support this condition as a synapomorphy.

In the full dataset, however, our results differed further from Gilbert et al. (2006) in the placement of three supposedly Cervinae species (*C. unicolor*, *C. eldi*, and *A. axis*) as sister to the remaining Cervidae. This renders both Cervinae and Plesiometa-*carpalia* paraphyletic in our full analyses and represents probably the greatest disagreement between our study and recent well supported phylogenies (Gilbert et al. 2006). All three species have short sequences, but in general clades within Cervidae are well supported in the full dataset. Here, we have a conflict between a study with more character data but fewer taxa (Gilbert et al. 2006) and one with a dense taxon sample but a single-gene. While it is not obvious what to conclude about this conflict, other than

Cervidae phylogenetics need further attention, our study by dense taxon sampling provides a particularly useful tool for comparative studies while we recommend adopting the Cervidae classification of Gilbert et al. (2006), until more detailed studies become available.

Within cetaceans, with the exception of Balaenopteridae and Eschrichtiidae (see May-Collado and Agnarsson, 2006), all families within Cetacea were recovered (Figs. 2 and 5d). The grey whale (*Eschrichtius*) the only member Eschrichtiidae consistently nested within Balaenopteridae as has been found in many other studies (e.g. Rychel et al., 2004; May-Collado and Agnarsson, 2006). Only fossil evidence still supports Balaenopteridae exclusive of *Eschrichtius* (Steeman, 2007), however, a more detailed combined analysis remains to be done.

The phylogenetic position of Platanistidae is perhaps the most disputed in Cetacean phylogenetics. In this study, it consistently placed sister to Delphina (recovering the clade Pandelphina as proposed by May-Collado et al., 2007). However, it is important to notice that the support, although consistent, is low (Fig. 5d and Table 2).

All analyses support the following relationship between the Delphinoidea families ((Delphinidae (Monodontidae + Phocoenidae) (Figs. 2 and 5d), previously found by both morphological and molecular analyses (e.g., Heyning, 1989; Waddell et al., 2000).

In general, subfamilies within Cetacea were also recovered (see May-Collado and Agnarsson, 2006 for discussion), while our results continue to reject the monophyly of the traditional subfamilies within Ziphiidae or Phocinae (Figs. 2 and 5d). The monophyly of and relationships among taxonomic groups within Ziphiidae thus remains unclear, as has been found in other recent studies (e.g. Dalebout et al., 2004). As for species relationships within Phocoenidae, our results are identical to a recent morphological phylogeny by Fajardo-Mellor et al. (2006). Within Delphinidae, our study supports the monophyly of subfamilies as proposed by LeDuc et al. (1999) with the following relationships suggested by the pruned datasets 1 and 2: (((Orcinae ((Globicephalinae (Stenoninae (Delphininae + Lissodelphininae)))))) (Figs. 2 and 5d). However, as pointed before by several authors (e.g. LeDuc et al., 1999; Price et al., 2005), the genera *Lagenorhynchus*, *Stenella*, and *Tursiops* appear not to be monophyletic. Our results, agreeing with LeDuc et al. (1999) suggest that *Lagenorhynchus acutus* and *Lagenorhynchus albirostris* (the type of the genus) are the only ‘true’ *Lagenorhynchus* species and may best be placed in their own subfamily (for example, *Lagenorhynchinae*). The remaining members of this genus should be transferred to *Cephalorhynchus* and included within Lissodelphininae. The phylogenetic relationships between subfamilies varied somewhat across analyses, particularly the placement of Orcinae (*Orcinus* and *Orcaella*), Lissodelphininae (*Lissodelphis*, *Cephalorhynchus*, and some species of *Lagenorhynchus*) was not consistent between analyses. Previous studies have not conclusively resolved relationships among dolphins and relatives either highlighting the need for further effort to better resolve delphinid phylogeny.

4.4. Extinct species

Our results agree with recent molecular studies that the recently extinct ‘mouse goat’ (*M. balearicus*) is not a goat (Lalueza-Fox et al., 2005). Our results, however, differ in the exact placement of *Myotragus*, placing it sister to the remaining Caprinae (Fig. 5b), instead of sister to sheep as found by Lalueza-Fox et al. (2005). Lalueza-Fox et al. (2005) included more character data, while we here include many more Caprinae species. Again, as it is well known that both adding characters and taxa can improve phylogenetic accuracy (see above) it is unclear which placement is more probable given the available evidence and we conclude that the exact placement of *Myotragus* remains an open question. The ‘Irish

Elk' or Giant Deer (Lister et al., 2005) (*M. giganteus*) in our study is sister to Père David's Deer (*E. davidianus*) together forming the sister clade to the remaining Cervinae (Fig. 5a). This contradicts the proposed sister relationship of *Megaloceros* and *Dama* found in previous studies (Lister et al., 2005; Hughes et al., 2006). Given that Lister et al. used both morphology and molecules their result may be more credible. However, Hughes et al. (2006) had a more complete taxon sampling (as we do as well) and were not able to conclusively place *Megaloceros*. In fact they found that a reasonable alternative placement of *Megaloceros* was sister to the remaining Cervinae, similar to what we find. Hence while clearly belonging to Cervinae, we may again conclude that the exact position of *Megaloceros* remains to be conclusively determined.

5. Conclusions

By analyzing a large number of cetartiodactylan species using a single mitochondrial gene our primary goal here is to provide a tool for species-level comparative studies. This approach offers rapid phylogenetic estimates for large clades, but may suffer by providing less reliable (less accurate) results than studies that include proportionally greater amount of character data. However, our results are, by and large, consistent with all major clades that can be treated as 'known' due to strong support from multiple lines of evidence in prior studies. This suggests that cytb performs extraordinarily well in resolving Cetartiodactyl phylogeny when taxon sampling is dense and reiterates arguments that adding taxa is as important a consideration as adding characters when the aim is to improve phylogenetic accuracy. Given that the phylogeny recapitulates current knowledge on higher level Cetartiodactyla phylogeny, it seems reasonable to expect the phylogeny as a whole to be a good working hypothesis and hence a useful tool. If cytb is similarly informative within related clades, an opportunity exists now to rapidly reconstruct detailed phylogenies of major mammalian clades to provide much needed tools for species-level comparative studies.

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