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ORIGINAL PAPER

The Evolution of Dental Eruption Sequence in Artiodactyls

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Abstract The sequence of eruption of the second generation of teeth varies across taxa, is highly functional, and is strongly influenced by genetic effects. We assessed postcanine dental eruption sequence across artiodactyls in order to test two hypotheses: 1) dental eruption sequence is a good phylogenetic character for artiodactyls; and, 2) eruption sequence is adaptive and associated with life history variables like postnatal growth and longevity in artiodactyls (Schultz's Rule). We examined postcanine eruption sequence in 81 genera (100 species) spanning ten families of Artiodactyla. Our ancestral state reconstruction supports the interpretation that the third molar erupted last in the ancestor of Artiodactyla, and that the fourth premolar erupted after the third molar in the ancestor of Ruminantia. Our results indicate that eruption of the third molar last evolved secondarily in the caprines, likely sometime in the Miocene. Overall, our results support the hypothesis that dental eruption sequence is phylogenetically conserved in artiodactyls. Caprines occupy high elevation habitats, and we hypothesize that evolution of their unique dental eruption sequence may be associated with limited resource availability in high elevation mountain systems and the necessity to process a wide range of vegetation types.

Keywords Caprinae · Phylogenetic signal · Ruminantia · Schultz's rule · Life history · Longevity · High elevation

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Introduction

Most mammals are diphyodont meaning they have two generations of teeth: the deciduous (milk) teeth and the adult teeth. These two generations of teeth allow for overall size and complexity to increase while growing from juvenile to adult, matching changes in overall body size and shape (Hillson 2005). The timing of tooth eruption is highly correlated between teeth, particularly in the postcanine dentition (Smith 1994), and is generally considered to be adaptive. This tight correlation is not surprising when considering that the timing of tooth eruption is constrained by many other factors, including the size of the face and dental arch, timing of permanent tooth development, juvenile and adult diets, life history, and even group dynamics, as represented by intrasex competition (Schultz 1935, 1956; Bryant 1990; Smith 1994, 2000; Leigh et al. 2008).

Many dental eruption studies have focused on primates and found that the sequence of eruption of the second generation of teeth varies across taxa, is highly functional, and is strongly influenced by genetic effects (Schultz 1935, 1956; Bryant 1990; Smith 1994, 2000; Wise et al. 2002; Suri et al. 2004; Leigh et al. 2008). There are generally two lines of thinking about dental eruption sequence: 1) dental eruption sequence is a good phylogenetic character in primates, and likely other mammals (Schwartz 1974; Tattersall and Schwartz 1974; Byrd 1981; Veitschegger and Sánchez-Villagra 2016), or 2) dental eruption sequence is adaptive and associated with life history variables like postnatal growth and longevity (Schultz 1956, 1960; Smith 1994, 2000).

Schultz (1956, 1960) originally hypothesized that dental eruption sequence is associated with the rate of postnatal growth in primates. This led to the proposal of Schultz's Rule, which states that replacement teeth erupt earlier in long-lived species with a slower rate of growth, also known as a slower life history (Smith 2000). As the molars have no deciduous complement in heterodont mammals (e.g., Osborn and Crompton 1973; Järvinen et al. 2009), the premolars are the replacement teeth of the postcanine dentition. Smith (2000) tested Schultz's Rule in ungulates and found that several faster-growing species erupt all the molars before other permanent teeth, while slower-growing species erupt the molars later in the sequence. Smith (2000) also found that maximum lifespan across 20 species of ungulates is significantly correlated with dental eruption sequence (calculated by the eruption of either I_1 or P_3 relative to the mandibular molars), suggesting that ungulates tend to follow Schultz's Rule, although primates appear to adhere to it even more so. In order to test the hypothesis that dental eruption sequence is a good phylogenetic character across mammals, we conducted a much more comprehensive examination of dental eruption sequence across artiodactyls and incorporated the most appropriate and up-to-date phylogenetic analyses.

Artiodactyls are a large group of hooved mammals (with more than 200 species; Geisler et al. 2007; Hassanin et al. 2012) that evolved approximately 70 Ma in Eurasia (Hassanin et al. 2012) and are nested paraphyletically within Artiodactyla (Geisler et al. 2007). The geographic origin of artiodactyls is somewhat obscured in the fossil record, as fossil artiodactyls have been recovered in North America, Europe, and Asia, all dated to the early Eocene (~55 Ma; Theodor et al. 2007). These small-bodied early artiodactyls have been classified taxonomically as Dichobunidae (McKenna and Bell 1997), or alternatively, broken down in two families, Dichobunidae and Diacodexeidae (Theodor et al. 2007). While artiodactyls are rare in the early Eocene, a presumed morphological radiation led to a diversity of forms by the middle Eocene (Theodor et al. 2007). Since then, Artiodactyla has diversified to include more than 200 extant terrestrial taxa, as well as the cetaceans (Geisler et al. 2007; Hassanin et al. 2012).

Artiodactyls are globally distributed, almost exclusively herbivorous, and play significant roles in their local ecosystems (Vrba and Schaller 2000a). Additionally, many species are habitat specialists that respond strongly to environmental change (e.g., Vrba and Schaller 2000a; Brooks et al. 2001; Buzan et al. 2013). With the exception of Suina, artiodactyls are obligate herbivores, and many of the groups have evolved specialized feeding techniques including a dependency on bacterial fermentation (Vrba and Schaller 2000a). As herbivorous grazers consuming large quantities of grasses and plant matter, artiodactyls have a significant impact on ecosystems and ecology (Owen-Smith et al. 2010), and grazing and foraging by artiodactyls has been linked to vegetation changes in density, succession sequence, and composition (e.g., Molvar et al. 1993; Bowyer 1997).

Artiodactyls also represent the group most heavily domesticated by humans: pigs, goats, sheep, cows, and llamas are some of the domestic artiodactyls utilized by humans around the world (Vrba and Schaller 2000a). The impact that artiodactyls have had in human history is unrivaled by any other mammalian group, in terms of agriculture and economics, as well as in environmental impact (Gentry 2000). The majority of human-use domestic animals are artiodactyls, and they serve as the world's largest source of farmed meat, milk, skins, and wools (Gentry 2000). Overall, artiodactyls as a group share many features including a generalized body plan, life history, and diet (Vrba and Schaller 2000a). Artiodactyls also have a well-sampled fossil record, and many share a relatively ancestral dental formula with teeth in all four dental classes (i.e., molars, premolars, incisors, and canines in some groups) (Hillson 2005).

Our work investigates generic-level variation in dental eruption sequence in artiodactyls. Previous work has demonstrated the modularity of the dentition in primates and mice, where the anterior teeth are genetically and phenotypically independent of the postcanine teeth (Hlusko et al. 2011). With this in mind, we restrict our study to the functional grinding teeth in herbivores, the postcanine dentition (premolars and molars). Specifically, we hypothesize that: H1) dental eruption sequence is phylogenetically conserved in artiodactyls, or more similar in more closely related genera, and H2) eruption of the third molar last is the ancestral condition in this group.

Materials and Methods

Materials

For this study, we examined postcanine dental eruption sequence in 81 genera (100 species) spanning ten families of Artiodactyla (Table 1). All examined specimens are held in the

Table 1 Number of genera and species sampled for this study

Clade	Family	Number of genera sampled	Number of species sampled
Artiodactyla	Antilocapridae	1	1
	Bovidae	43	56
	Camelidae	3	3
	Cervidae	18	23
	Giraffidae	2	2
	Hippopotamidae	2	2
	Moschidae	1	1
	Suidae	5	6
	Tayassuidae	3	3
	Tragulidae	3	3
	Total	81	100

collections of the Museum of Vertebrate Zoology, Berkeley, CA (n = 726) or the National Museum of Natural History, Washington, D.C. (n = 3445). We visually examined specimens across ontogenetic stages. Eruption sequence was defined as either having the third molar erupt before the fourth premolar, vice versa, or simultaneous (Fig. 1). When eruption of the fourth premolar and third molar seemed to be at the same stage in multiple specimens, the dental eruption sequence for the genus was scored as simultaneous. At least two occurrences of eruption sequence for each genus were required to confidently assess the relationship between eruption of the fourth premolar and the third molar (exceptions are *Bos, Bubalus*, *Catagonus*, *Hippocamelus*, *Hylochoerus*, *Nilgiritragus*, *Ozotoceros*, *Pelea*, *Phacochoerus*, *Pseudois,* and *Rucervus*; Table 2). We examined eruption sequence in both the maxilla and mandible of each specimen where available, and from here forward, we use the mandibular notation (tooth type abbreviation followed by tooth number in subscript) when discussing particular teeth. While we found no difference in eruption sequence between maxilla and mandible, we did note that eruption tends to occur earlier in the mandible than in the maxilla of an individual.

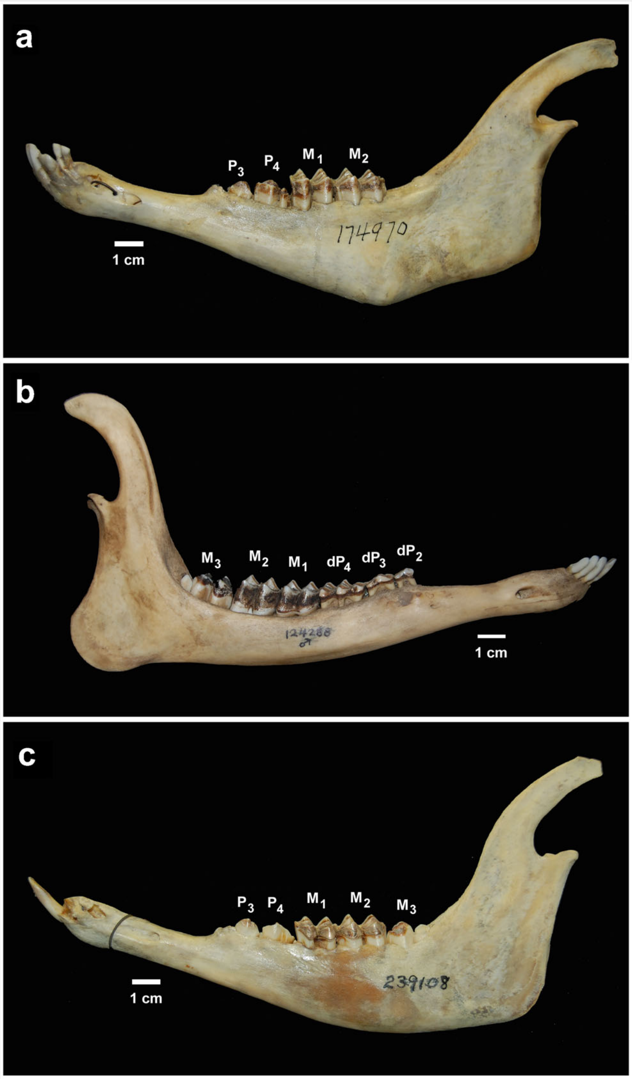

Fig. 1 Examples of different eruption sequences in the mandibles of terrestrial Artiodactyla. **a** Eruption of the M_3 last in *Capra caucasica*. **b** Eruption of the P_4 after the M_3 in *Odocoileus hemionus*. **c** Simultaneous eruption of M_3 and P_4 in *Oreamnos americanus*. M is molar, P is premolar, d is deciduous, and the number denotes tooth number. E.g., dP_4 is deciduous premolar 4

Intraspecific Variation in Dental Eruption Sequence

We systematically surveyed all *Ovis* craniodental specimens available at the Museum of Vertebrate Zoology (*Ovis canadensis* n = 176, *Ovis dalli* n = 9) to assess intraspecific variation in dental eruption sequence. We classified the state of eruption of each postcanine tooth from 1 to 3, where a score of 1 is unerupted, 2 is erupting, and 3 is fully erupted. Our definition of erupting (Score 2) is when the tooth has erupted above the level of the maxilla/mandible when viewed lingually, but is not yet fully erupted. All four postcanine quadrants were scored when available (left and right, maxillary, and mandibular). In cases where a tooth was missing by wear, but the rest of the jaw was clearly fully erupted and fully worn, a score of fully erupted was given for that tooth.

Of the 185 *Ovis* specimens systematically surveyed at the MVZ, n = 48 are in the process of erupting one or more of the postcanine teeth. The sample is further reduced when comparing third molar and fourth premolar eruption. Only n = 15 specimens, all *Ovis canadensis*, are in the process of erupting either the fourth premolar, the third molar, or both. Within that small sample, n = 4 specimens show the fourth premolar fully erupted while the third molar is still in the process of erupting. There is no variability among these four specimens: all postcanine teeth are fully erupted except the third molar. In contrast, not a single specimen has a third molar that is fully erupted while the fourth premolar is still erupting or unerupted. Within this large sample size, we find no variability in the phenotype of the third molar erupting last. Based on this analysis, we are confident in assuming that our determination of eruption sequence based on sample sizes of at least two observations is fairly sound. Given the large sample sizes needed to test this more fully, absolute certainty will be difficult to accomplish. The full data from the test for intraspecific variation are available in Online Resource 1.

Ancestral State Reconstruction

In order to quantify the evolutionary context of the phenotype, we ran an ancestral state reconstruction using the distribution of extant dental eruption sequences. Also known as character mapping, ancestral state reconstruction statistically predicts the state of each node in the phylogeny based on the distribution of eruption sequences across extant taxa (Felsenstein

Table 2 Dental eruption sequences for the species sampled in this study

Family	Genus	Species[a]	N=[b]	P_4 later	M_3 later	Simultaneous
Antilocapridae	*Antilocapra*	*americana*	2	X		
Bovidae	*Aepyceros*	*melampus*	3	X		
	Alcelaphus	*buselaphus, lichtensteinii*	3	X		
	Antidorcas	*marsupialis*	4	X		
	Bison	*bison*	4	X		
	Bos	*grunniens*	1	X		
	Bubalus	*bubalis*	1	X		
	Budorcas	*taxicolor*	3	X		
	Capra	*hircus, caucasica*	3		X	
	Cephalophus	*weynsi*	2	X		
	Connochaetes	*taurinus*	3	X		
	Damaliscus	*korrigum*	4	X		
	Gazella	*arabica, bennettii, dorcas*	5	X		
	Hemitragus	*jemlahicus*	2		X	
	Hippotragus	*equinus, niger*	4	X		
	Kobus	*ellipsiprymnus*	4	X		
	Litocranius	*walleri*	6	X		
	Madoqua	*guentheri, kirkii*	3	X		
	Naemorhedus	*griseus, *C. milneedwardsii, *C. sumatraensis*	5	X		
	Neotragus	*pygmaeus*	2	X		
	Nesotragus	*moschatus*	2	X		
	Nilgiritragus	*hylocrius*	1		X	
	Oreamnos	*americanus*	2			X
	Oreotragus	*oreotragus*	5	X		
	Oryx	*beisa, dammah, gazella*	4			X
	Ourebia	*ourebi*	4			X
	Ovibos	*moschatus*	4	X		
	Ovis	*aries, canadensis*	5		X	
	Pelea	*capreolus*	1	X		
	Pseudois	*nayaur*	1	X		
	Raphicerus	*campestris*	6	X		
	Redunca	*fulvorufula, redunca*	2	X		
	Rupicapra	*rupicapra, pyrenaica*	3	X		
	Sylvicapra	*grimmia*	4	X		
	Syncerus	*caffer*	4	X		
	Taurotragus	*oryx*	3	X		
	Tragelaphus	*scriptus*	4	X		
Camelidae	*Lama*	*glama*	2		X	
Cervidae	*Alces*	*americanus*	2	X		
	Cervus	*elaphus*	3	X		
	Elaphodus	*cephalophus*	3	X		
	Hippocamelus	*antisensis*	1	X		
	Hydropotes	*inermis*	2	X		
	Mazama	*americana, rufina, temama*	5	X		
	Muntiacus	*muntjac, reevesi*	2	X		
	Odocoileus	*hemionus*	3	X		
	Ozotoceros	*bezoarticus*	1	X		
	Pudu	*puda, mephistophiles*	2	X		
	Rangifer	*tarandus*	4	X		

Table 2 (continued)

Family	Genus	Species[a]	N=[b]	P_4 later	M_3 later	Simultaneous
	Rucervus	*eldii*	1	X		
	Rusa	*timorensis, unicolor*	3	X		
Hippopotamidae	*Hippopotamus*	*amphibius*	2		X	
Moschidae	*Moschus*	*berezovskii*	2	X		
Suidae	*Babyrousa*	*babyrussa, celebensis*	2		X	
	Hylochoerus	*meinertzhageni*	1		X	
	Phacochoerus	*aethiopicus*	1		X	
	Potamochoerus	*porcus*	2		X	
	Sus	*scrofa*	10		X	
Tayassuidae	*Catagonus*	*wagneri*	1		X	
	Pecari	*tajacu*	2		X	
	Tayassu	*pecari*	4		X	
Tragulidae	*Tragulus*	*kanchil*	3	X		

[a] Only species and genera for which we were able to confidently assess dental eruption sequence are included in this table

[b] Sample size of specimens used to determine dental eruption sequence in this study

*An asterisk denotes a species with an alternate genus-level classification

1985; Coddington 1988; Donoghue 1989). For this reconstruction, we mapped the dental eruption sequences onto the artiodactyl phylogeny by creating a character state matrix. We ran the ancestral state reconstruction in Mesquite with the Mk1 likelihood method (Maddison and Maddison 2015) using molecular data (six autosomal and 14 mitochondrial genes) from the 10ktrees database (Arnold et al. 2010). In cases where we have phenotypic data for a species but molecular data are not available, we used congeners in the phylogeny (marked by an asterisk). We also ran the ancestral state reconstruction using parsimony, but it gave the same results and we decided to defer to the likelihood method for further analysis. It is important to note that debate continues on the phylogenetic relationships between crown artiodactyls. In particular, the exact timing and sequence of divergence of Suina, Camelidae, Hippopotamidae, and Ruminantia are still under considerable debate (Matthee et al. 2001; Murphy et al. 2001; Spaulding et al. 2009; Meredith et al. 2011; Zhou et al. 2011; Hassanin et al. 2012). We chose to use the phylogeny from 10ktrees, and the divergence of Suina is placed basal to Camelidae and Hippopotamidae in this study. Specimens classified as "likely" erupting P_4 after M_3 were excluded from the ancestral state reconstruction.

Test for Phylogenetic Signal

In order to test for phylogenetic signal in dental eruption sequence, we ran the D-statistic in the R statistical program v3.1.2 (R Core Team 2016) using *caper* (Orme et al. 2015). The D-statistic tests the hypothesis that a phenotype is more phylogenetically conserved across the tree than expected under Brownian motion (Orme et al. 2015). The D-statistic is used expressly for binary traits and was therefore only applied to dental eruption sequence in this study. A D-value less than 1 indicates phylogenetic conservatism relative to random Brownian motion (Orme et al. 2015).

To test the non-binary life history and body size traits, we ran a Blomberg's K analysis using phylosignal in the *picante* package (Kembel et al. 2010). Blomberg's K tests whether a particular character is present in related taxa more frequently than expected by Brownian motion (Blomberg et al. 2003). The K-value for a trait can be either greater than 1, equal to 1, or less than 1. A K-value of K = 1 generally indicates neutral evolution of the trait, while K > 1 generally suggests that the trait is phylogenetically conserved relative to Brownian motion. In contrast, K < 1 is generally interpreted as less associated with phylogeny than expected from the null, although rapid divergence or heterogeneous rates of genetic drift can also result in a low K-value (Blomberg et al. 2003; Revell et al. 2008).

For these phylogenetic analyses, we trimmed the tree down to only those species for which dental eruption sequence was confidently assessed (i.e., not "likely" or simultaneous), and for which molecular data were available. In order to account for phylogenetic uncertainty, we ran both the D-statistic and Blomberg's K through 25 iterations, using 25 of the likely phylogenies generated by the 10ktrees analyses. The averages of the 25 iterations were taken as our values of D and K for analysis of phylogenetic signal.

Life history and body size variables. We collected life history and body size data for the majority of artiodactyls included in this study. Ranges for each trait were taken from the literature, with the exception of average maximum lifespan, the ranges for which were collected from AnAge, part of the Human Ageing Genomic Resources database (Tacutu et al. 2013). For this study, we investigated average maximum lifespan, litter size, length (cm), height (cm), and body weight (cm). Body weight values were taken from the average for the male of the species, but length and height values were not specified by sex. All values, with the exception of litter size, were log-transformed for the analyses. We calculated phylogenetic independent contrasts across our phylogenetic tree using the *ape* package in R (Paradis et al. 2004). This statistic allows for the comparison of means between traits while taking into account the phylogeny and the number of independent trait occurrences (Ricklefs and Starck 1996). All independent contrasts were run through 100 iterations to account for phylogenetic uncertainty. Raw data and references for life history and body size variables are available in Online Resource 2.

Results

Variation in Eruption Sequence across Artiodactyls

We definitively assessed postcanine eruption sequence in 62 genera (81 species). Of those, 45 genera have a sequence where the fourth premolar (P_4) erupts later than the third molar (M_3), 14 have a sequence where the M_3 erupts last, and three have a sequence with approximately simultaneous eruption of P_4 and M_3 (Table 2). We found four more genera that likely have the P_4 erupting after the M_3, and one genus that likely has the M_3 erupting last, but we need a larger sample size to definitively confirm these sequences. We were unable to definitely assess dental eruption sequence in 14 genera based on a lack of available specimens at appropriate ontogenetic stages. We found no evidence of intrageneric variation in dental eruption sequence in this study.

Overall, we successfully sampled the breadth of the artiodactyl phylogeny, and our results clearly demonstrate a phylogenetic pattern (Fig. 2). Genera sampled in Artiodactyla families Camelidae, Hippopotamidae, Suidae, and Tayassuidae all erupt the third molar last. In contrast, nested within the artiodactyl clade, Ruminantia families Bovidae, Moschidae, Cervidae, Antilocapridae, and Tragulidae almost exclusively erupt the P_4 last, although there are some exceptions. Of the 52 ruminant genera we examined, 45 erupt the P_4 last. The exceptional genera are *Capra*, *Hemitragus*, *Nilgiritragus, Oreamnos*, *Oryx*, *Ourebia,* and *Ovis.*

Capra, *Hemitragus, Nilgiritragus,* and *Ovis* all erupt the M_3 last, uniquely among Ruminantia. These four genera are all part of subfamily Caprinae. Due to small sample sizes, we were unable to definitely assess dental eruption sequence in some of the other members of Caprinae (*Arabitragus*, *Ammotragus*, and *Pantholops*). But several of the caprine genera sampled here erupt the M_3 last. Based on the distribution of dental eruption sequences across the artiodactyl phylogeny, and supported by our ancestral state reconstruction, the eruption of the M_3 last is either a reversal to the ancestral state, or secondarily derived, in subfamily Caprinae.

Oryx, *Ourebia,* and *Oreamnos* appear to erupt the P_4 and M_3 approximately simultaneously, but this approximation could be the result of limited sample size. With a larger sample spanning a greater ontogenetic timeframe, it may be possible to refine this approximation and definitively assess whether the P_4 or M_3 erupts later. *Oryx* (tribe Hippotragini) and *Ourebia* (tribe Antilopini) are both African bovids with a primary diet of grasses supplemented by other vegetation. Recent analyses suggest that Hippotragini and Antilopini diverged 15 to 13 Ma (Bibi 2013). There is some suggestion in the literature that *Oreamnos* may erupt the M_3 after the P_4 (Brandborg 1950), but other reports are contradictory (Kerr 1966). The North American mountain goat (*Oreamnos americanus*) is closely related to *Capra, Hemitragus, Ovis,* and other genera in subfamily Caprinae. Overall, our data show that subfamily Caprinae is unique among Ruminantia in having a cluster of genera that erupt the M_3 last (*Capra, Hemitragus, Nilgiritragus* and *Ovis)*, as well as one with simultaneous eruption (*Oreamnos*).

Ancestral State Reconstruction

Our ancestral state reconstruction supports that the third molar erupted last in the ancestor of Artiodactyla with 89.0% likelihood (Fig. 2; Table 3). An equally high likelihood of 86.1% supports that the ancestor of artiodactyls (excepting Suina) erupted the third molar last. The likelihood of the third molar erupting last is reduced to 78.8% for the ancestor of Ruminantia + Hippotamidae. After the divergence of Hippotamidae, our ancestral state reconstruction finds 87.4% likelihood that the P_4 erupted after the M_3 in the ancestor of Ruminantia. It is important to note that, as our test of intraspecific variation was completed in a ruminant taxon, it is possible that non-ruminant artiodactyls are more variable in their eruption sequence. Greater sampling, particularly of Camelidae and Hippopotamidae, and their fossil relatives, will further resolve the support for changes in dental eruption sequence at more basal nodes of the phylogeny.

The most likely character state is more ambiguous at the base of subfamily Caprinae. Greater sampling, as well as a more resolved phylogeny, could likely clarify the state at these nodes. Our ancestral state reconstruction supports that the ancestor of Caprinae is 0.0% likely to have erupted the third molar last. The likelihood that the third molar erupted last at the node between *Pseudois* and *Capra* is slightly higher at 1.3%. It is not until the ancestor of *Hemitragus* and *Capra* that we find 98% likelihood that the third molar erupted last. A similar pattern is found along the branch of the phylogeny leading to *Ovis* and *Nilgiritragus*.

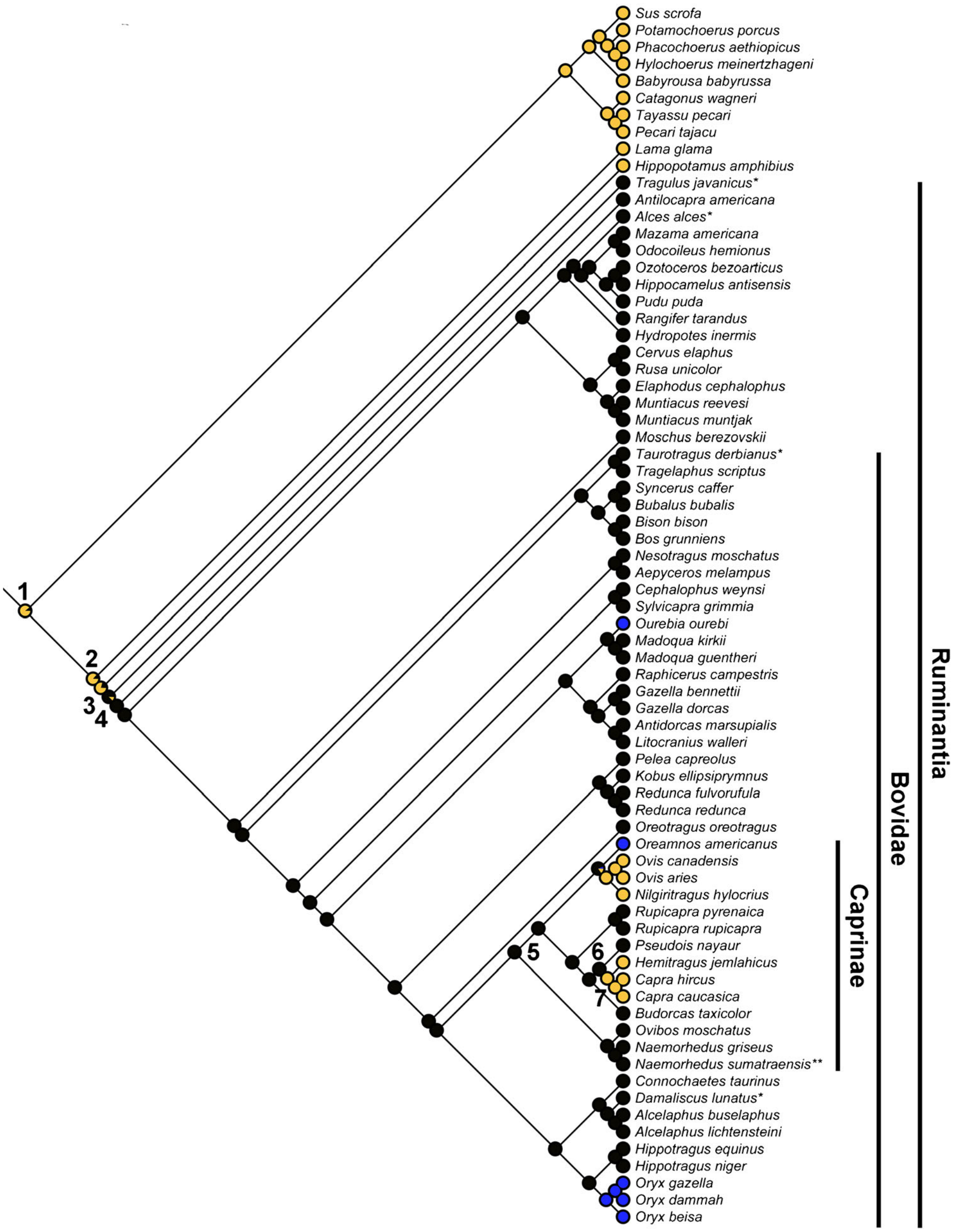

Fig. 2 Ancestral state reconstruction of dental eruption sequence across Artiodactyla. *Yellow* indicates that the third molar (M_3) erupts last. *Black* indicates that the fourth premolar (P_4) erupts after the M_3. *Blue* indicates that M_3 and P_4 erupt simultaneously. See methods for information about construction of the phylogeny. See Table 3 for dates and likelihoods at numbered nodes. Asterisks denote congeners used in place of related species for which we have phenotypic but no molecular data. *Double asterisks* denote species with an alternate genus level classification

Table 3 Likelihood (%) of each dental eruption sequence at each ancestral state node on the phylogeny

ASR Node[a]	Likelihood that M_3 erupts after P_4	Likelihood that P_4 erupts after M_3	Likelihood of simultaneous eruption	Diverging branch	Geologic date	Reference
1	89.0%	9.8%	1.2%	Suina	>65 Ma	Kumar and Hedges 1998
2	86.1%	13.1%	0.8%	Camelidae	>55 Ma	Zhou et al. 2011
3	78.8%	20.5%	0.8%	Hippopotamidae	~55 Ma	Hassanin et al. 2012
4	12.1%	87.4%	0.5%	Tragulidae	~45 Ma	Fernandez and Vrba 2005
5	0.0%	100.0%	0.0%	*Naemorhedus* + *Ovibos*	~14.5 Ma	Fernandez and Vrba 2005
6	1.3%	98.7%	0.0%	*Pseudois*	~11.2 Ma	Fernandez and Vrba 2005
7	98.0%	1.9%	0.0%	*Hemitragus*	~8 Ma	Fernandez and Vrba 2005

[a] ASR Node refers to Fig. 2

Test for Phylogenetic Signal

All of the life history and body size variables analyzed here have a significant phylogenetic signal ($p < 0.05$), meaning that the distribution of each trait across the phylogeny is significantly different from a neutral model of Brownian motion (Table 4). Dental eruption sequence is very phylogenetically conserved (D-value <0). Average litter size is also phylogenetically conserved (K-value 1.20). A K-value <1 is indicative of a trait being less phylogenetically conserved than expected when compared to the neutral model of Brownian motion, although low K-values can also result from rapid divergence or heterogeneous rates of genetic drift (Revell et al. 2008). Average body weight, height, length, and maximum lifespan all have K-values significantly less than 1 in this study. Overall, average height and length have the lowest K-values, and, with the exception of dental eruption sequence, average litter size is the only life history or body size trait with a K > 1, suggesting strong phylogenetic signal for this trait.

Life History and Body Size Variables

Although the life history and body size variables have significant phylogenetic signals, none of them are significantly correlated with dental eruption sequence. None of the phylogenetic independent contrasts between life history or body size variables and dental eruption sequence in artiodactyls are significant (Table 5). These data suggest that dental eruption sequence and the life history and body size variables sampled here, including maximum lifespan, are not correlated.

Discussion

Our results demonstrate that eruption of the fourth premolars after the third molars is an apomorphy for Ruminantia within Artiodactyla. Based on the fossil record and molecular data for this group, this eruption sequence probably evolved ~40–55 Ma (Gentry 2000; Métais and Vislobokova 2007; Hassanin et al. 2012). The fossil record of Ruminantia extends to approximately 55 Ma, spanning North America and Asia (Métais and Vislobokova 2007; Theodor et al. 2007). Within the extant artiodactyls, the ruminant clade is comprised of all artiodactyls excepting the suids, tayassuids, hippopotamids, and camelids, and is defined by three primary hard tissue features: the fusion of the cuboid and navicular tarsals, the loss of upper incisors, and the incisiform lower canines (Métais and Vislobokova 2007). Ruminantia are also characterized by a suite of morphological and behavioral phenotypes that are associated with their unique diet and obligate herbivory (Vrba and Schaller 2000a). We would add eruption of the fourth premolar after the third molar to this list, excepting subfamily Caprinae and the two bovid genera with simultaneous eruption.

We find no evidence that major life history or body size variables correlate with this difference in eruption sequence. Rather, the synapomorphic chewing complex shared by Ruminantia may have played a role in the evolution of this derived dental eruption sequence. Evolution of delayed premolar eruption in the ancestor of Ruminantia may be associated with diet, jaw morphology, and/or the biomechanics of chewing. Ruminantia are characterized by an unfused mandible and forward placement of the masseter muscle, one of the most important chewing muscles in mammals (e.g., Janis 1995; Hogue and Ravosa 2001). Additionally, interproximal tooth wear at the junction between the P_4 and M_1 is common in Ruminantia (pers. obs.), frequently resulting in a marked concavity. This suggests that factors such as intense chewing strain and force during feeding, enamel thickness, and mesial drift may contribute to extensive wear at the P_4/M_1 junction (Fortelius 1985; Pfretzschner 1992; Macho and Berner 1993). Later eruption of the fourth premolars may have evolved as a buffer to this strain, ensuring that a strong chewing surface is available for a longer period of time before wear causes serious problems and even death.

The early Miocene was characterized by a period of relatively warm and stable temperatures, referred to as the Miocene Climatic Optimum (Böhme 2003). During this Optimum (17–15 Ma), many groups of animals, including the artiodactyls, radiated rapidly, evolving new traits and exploiting the new habitats created by changing climate and vegetation shifts (Janis 1989; Zachos et al. 2001; Zhou et al.

Table 4 Results from the tests of phylogenetic signal. All *p*-values are significant

Life history trait[a]	Blomberg's K	K *p*-value	D statistic	D *p*-value
P_4 erupts after M_3	-	-	-1.217	0.005
Average weight (kg)	0.523	0.001	-	-
Average litter size	1.263	0.001	-	-
Average height (cm)	0.440	0.001	-	-
Average length (cm)	0.490	0.001	-	-
Average maximum lifespan (yr)	0.607	0.001	-	-

[a] All values for continuous traits were log-transformed

Table 5 Sample size (species) and descriptive statistics for each life history and body size trait, by dental eruption sequence

Life history/body size trait[a]	P_4 erupts last N=	Mean	Median	Range	M_3 erupts last N=	Mean	Median	Range	PIC*
Average maximum lifespan (yr)	40	21.5	21.9	25.6	14	26.1	22.4	43.9	0.935
Average height (cm)	41	86.8	84.0	160.0	11	91.1	82.5	82.5	0.528
Average length (cm)	41	146.4	140.0	232.5	9	168.4	171.0	176.5	0.261
Average weight (kg)	43	153.0	50.0	948.0	16	197.2	83.3	1777.0	0.583
Average litter size	43	1.0	1.0	1.0	16	1.9	1.3	4.0	0.929

[a] Raw data for life history and body size traits are available in Online Resource 2

*The phylogenetic independent contrast (PIC) is the *p*-value for a comparison between the mean of each trait and dental eruption sequence (Ricklefs and Starck 1996); no PICs are significant

2012). Changes in pressure systems also changed aridity in other areas of the world expanding open grasslands, savannah, and steppe plains at both high and low elevations (Janis 1989). After the warmer Miocene, temperatures cooled in the early Pliocene resulting in the further spread of grasslands (Strömberg 2011). Also during this time, the uplifting of mountain ranges like the Himalayas, the East African Rift System, and the Rockies created new mountain habitats yet to be occupied by the radiating artiodactyls (Wolfe 1985; Janis 1989). As competition increased, the ancestor of the caprines moved into a high elevation niche, likely exploiting this novel habitat in response to changing ecosystems.

Our results indicate that either an evolutionary reversal or a secondary evolution of the ancestral dental eruption sequence occurred in subfamily Caprinae at least once and possibly twice. Based on our ancestral state reconstruction, the ancestor of *Hemitragus* and *Capra* was erupting the third molar last with 98.0% likelihood. The molecular split between these two genera likely occurred ~4.5 Ma (Ropiquet and Hassanin 2005), although fossils date the first appearance of *Capra* around 1.9 Ma (Bibi et al. 2012). Molecular data and the fossil record place the evolution of subfamily Caprinae sometime in the Miocene, approximately 6–15 Ma: the wide range reflects the range of opinions on the precise date (Fernández and Vrba 2005; Lalueza-Fox et al. 2005; Ropiquet and Hassanin 2006). The earliest fossil occurrence of subfamily Caprinae is hypothesized to be *Protoryx enanus* from the middle Miocene of Europe (Köhler 1987; Gentry and Heizmann 1996). Like many ungulate groups, caprines underwent a major radiation in the Miocene (Gentry 2000; Vrba and Schaller 2000b). The exact phylogenetic relationships of extant taxa in subfamily Caprinae are still under much debate (e.g., Hassanin et al. 1998; Hassanin and Douzery 1999; Shafer and Hall 2010; Bibi 2013).

To this day, caprines are characterized by their utilization of high elevation habitats, rare among artiodactyls, and they can be found at the tops of mountains around the world (Vrba and Schaller 2000b). Vegetation quality, density, and composition changes along an altitudinal gradient (Vázquez and Givnish 1998; Shaheen and Shinwari 2012). The vegetation at high elevations is less diverse (e.g., Tranquillini 1964), and many plants die back completely under the snow (e.g., Khan et al. 2013). It is possible that evolution of the unique dental eruption sequence in caprines may be associated with resource availability in high elevation habitats. A shift in diet due to ancestral changes in habitat occupation may have altered the chewing stroke and bite force in goats and their relatives. Later eruption of the third molars guarantees that grinding teeth will be available longer in the lifespan of the animal, potentially improving overall fitness. There are a few other unique ruminants that occupy high elevation niches, particularly in the Tibetan plateau (e.g., cervid *Cervus albirostris* [formerly *Przewalskium*], bovid *Bos mutus*, and caprine *Pantholops hodgsonii*; Leslie 2010; Ge et al. 2013), but we were not able to sample these taxa in the current study. Their rarity is reflected in their poor representation in many museum collections. Further work examining these high elevation species, as well as directly comparing the quality and diversity of diets in Caprinae compared to other high elevation and non-elevation ruminants, will allow for more thorough testing of this hypothesis.

Fossil Evidence

An overview of artiodactyl fossil evidence supports the timeline produced by our ancestral state reconstruction. Fossil suid specimen KNM-SH 38051 (*Nyanzachoerus*), a right mandible with P_4-M_3, clearly shows the fourth premolar erupted and in occlusion while the third molar is still in the process of erupting (Tsujikawa 2005). This Miocene fossil provides evidence that suids have been erupting the third molar last for at least ten million years, and likely since their purported divergence with the ancestral artiodactyl group in the Eocene (Kumar and Hedges 1998). In contrast, *Diplobune*, a European artiodactyl that lived approximately 35 Ma, erupted the fourth premolars after the third molars (Sudre 1974; Blondel 2001; Erfurt and Métais 2007). The date of this fossil and dental eruption sequence accord directly with our ancestral state reconstruction detailing the evolution of this phenotype approximately 40–55 Ma, and suggest that either this trait is homoplastic or that *Diplobune* may have been a ruminant.

While we were unable to definitively assess dental eruption sequence for extant Giraffidae in this study, personal examination of a fossil giraffe from the Pleistocene of Ethiopia (BOU-VP-1/30) gives at least one example of dental eruption sequence in this group. BOU-VP-1/30 is an excellently preserved right maxilla that clearly shows the M_3 fully erupted while the P_4 is in the process of erupting. This fossil provides some limited evidence that Giraffidae, like other ruminants, likely erupts the P_4 after the M_3.

Fossil evidence from subfamily Caprinae also supports the results of our ancestral state reconstruction. *Myotragus,* a fossil goat from the Balearic Islands of Spain, erupts the third molars last like other extant caprines (Jordana et al. 2013). This extinct animal lived exclusively on the Balearic Islands from approximately 5 Ma until about 10,000 years ago (Jordana and Köhler 2011). Interestingly, eruption of the third molars in this island goat is even later than is seen in the rest of the subfamily (Bover and Alcover 1999; Jordana and Köhler 2011). Jordana and Köhler (2011) argued that the limited resources of the island habitat further influenced the timing of eruption in this group.

Conclusion

These data show a clear phylogenetic signal for variation in dental eruption sequence across Artiodactyla. All four extant artiodactyl families basal to Ruminantia erupt the third molar last (Suidae, Tayassuidae, Camelidae, and Hippopotamidae). In contrast, almost all Ruminantia erupt the fourth premolar after the third molar. Based on fossil and molecular evidence, the character state change, from erupting M_3 last to erupting P_4 after the M_3, occurred in the ancestor of Ruminantia between 40 and 55 Ma, during the Eocene.

Uniquely among Ruminantia, four genera in subfamily Caprinae erupt the third molar last. Another genus in the subfamily has almost simultaneous eruption of the fourth premolar and third molar, a character state that is relatively rare among artiodactyls. Parsimony suggests that the evolution of this dental eruption sequence, either as a reversal or a secondary derivation, occurred at least once and possibly twice in the Miocene ancestors of *Capra* and *Ovis*.

Overall, these data support the hypothesis that dental eruption sequence is phylogenetically conserved in artiodactyls, and fail to support the hypothesis that either lifespan or other life history and body size traits are significantly associated with dental eruption sequence. In the case of the artiodactyls, Schultz's Rule does not apply. By highlighting a dental trait with a strong phylogenetic signal that extends into the Eocene, we offer an additional phenotype that can be used to weigh in on ongoing phylogenetic debates about relationships among extant and extinct taxa. As we explore the phylogenetic signal of dental eruption sequence in other taxa, we will be able to better understand the potential drivers of variation in this trait.

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Author Contributions TAM collected the data, conducted the analyses, and wrote the manuscript. LJH supervised the project and edited the manuscript.

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