

# Tooth Eruption Sequences in Cervids and the Effect of Morphology, Life History, and Phylogeny

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Published online: 17 November 2015  
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**Abstract** Tooth eruption sequences vary in a non-random way among mammalian species. Several variables have been linked to this, including tooth and jaw shape, adaptations to diet, and food processing. Likewise, changes in eruption patterns correlate with the speed of postnatal growth in some groups, the Schultz's Rule pattern. Here, the eruption pattern of the permanent dentition in lower jaws from different cervid species have been investigated to discern the effect of these factors and phylogeny as well as to reconstruct the ancestral tooth eruption sequence of cervids. In ruminants, the different patterns of emergence of permanent teeth seem to be best explained by phylogeny. The degree of hypsodonty, age of first molar eruption, and life history parameters such as longevity and age of female sexual maturity do not explain the observed sequential differences in eruption patterns. The Parsimov-based analysis for the ancestral state resulted in a tooth eruption sequence of m1 – m2 – i1 – i2 – i3 – c – m3 – (ppp) for Cervidae; a pattern recorded in *Odocoileus*, *Capreolus*, and *Hydropotes*. The eruption pattern of *Caenomeryx filholi*, from the Oligocene of Gaimersheim, is identical to the result of the Parsimov-based analysis except for the presence of a first premolar, a tooth lost in cervids.

**Keywords** Parsimov-based genetic inference (PGi) · Continuous analysis · Heterochrony · Schultz's Rule · Ruminantia

## Introduction

Mammals replace their teeth only once during their life, possessing milk (deciduous) and adult (permanent) dentitions, but molars have only one generation (e.g., Osborn and Crompton 1973). The relative sequence of permanent tooth eruption is not fixed and varies among species (e.g., Smith 2000). Several hypotheses as to why these sequential differences occur have been postulated (e.g., Slaughter et al. 1974; Tattersall and Schwartz 1974; Simpson et al. 1990; Smith 2000; Godfrey et al. 2005). The aim of this study was to document the patterns of variation in eruption sequences in a clade of mammals and to investigate the variables associated with that variation. For this, the lower jaws of cervids were studied and compared with other members of Ruminantia. The general tooth formula in the lower jaw of cervids as well as ruminants is three incisors, one canine, three premolars, and three molars (Thenius 1989) and few species such as *Myotragus*, *Connochaetes*, or *Antidorcas* have a different dental formula (Rautenbach 1971; Attwell 1980; Jordana et al. 2013). Other shared features are an incisiform canine followed by a diastema, selenodont tooth morphology, and two distinct sets of functional teeth (van Nievelt and Smith 2005a). Nonetheless, Ruminantia do not share the same eruption pattern (e.g., Smith 2000), which allows testing for different signals such as phylogeny and anatomy as well as ecological and life history variables. In contrast, carnivorans and primates are more variable in the arrangement of teeth within the lower jaw as well as in morphology and the expression of the two sets of teeth (Thenius 1989; van Nievelt and Smith 2005a).

**Electronic supplementary material** The online version of this article (doi:10.1007/s10914-015-9315-8) contains supplementary material, which is available to authorized users.

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## Morphological Constraints, Adaptive Evolution, and Dental Eruption Patterns

The idea that the general facial architecture could influence the pattern of dental eruption was proposed based on the study of ape and hominid remains (Simpson et al. 1990). It was assumed that the human pattern of building and replacing teeth is influenced by three major factors: the reduction of the canine tooth in males, the reduction of prognathism in the hominid lineage, and the peculiarity of the human m3 (Simpson et al. 1990). Tooth morphology and size may also affect the sequential differences in tooth eruption. Slaughter et al. (1974) investigated the eruption sequence of the postcanine teeth in Afrotheria, Carnivora, Eulipotyphla, Leptictida, and Scandentia and concluded that the sequential differences are related to the different morphology of the teeth, especially the carnassials in carnivorans. In Multituberculata, the increasing size of the lower fourth premolar is considered to be causally coupled to several changes within the eruption pattern (Greenwald 1988). Other hypotheses with a more adaptive value have also been discussed in marsupial and placental mammals. One example is the relative delay of development and eruption of certain incisor teeth in marsupials and carnivorans. A late eruption of certain incisors has been linked to suckling, as the resulting open space could allow for a longer preweaning period (Luckett and Wooley 1996; van Nievelt and Smith 2005a, b). Besides that, diet and food processing have been linked with permanent tooth eruption patterns (Godfrey et al. 2001; Dirks 2003; Guthrie and Frost 2011; Forasiepi and Sánchez-Villagra 2014).

## Life History and Dental Eruption Patterns

It has been shown in primates that some life history variables such as brain mass and weaning period correlate with the age of first permanent tooth eruption (Smith 1992; Smith et al. 1994; Godfrey et al. 2001). However, not only the time but also the pattern of eruption is variable even in closely related species. To explain this, Smith (2000) postulated Schultz's Rule based on the work of Adolph Schultz (1956, 1960). According to it, an animal with a slower and longer life history has a tendency to replace deciduous teeth early in the relative sequence of tooth eruption compared to eruption of molar teeth. Therefore, Schultz's Rule would reflect the dynamics between the decay of the deciduous teeth and the possibility for the jaw to accommodate molar teeth in a slow growing mammal. Fast growing mammals would not have such physical constraints because speed of jaw growth to accommodate the molar teeth would precede the loss of functionality in the deciduous dentition. The validity of Schultz's Rule has been tested on "ungulates" and primates with a strong support found in primates and "generalized ungulates" such as Suinae but with a weaker support in more "specialized ungulates" such as Ruminantia (Smith 2000). Subsequently, several studies

examined this "rule." Some argued in favor of this hypothesis based on studies on platyrrhines (Henderson 2007), pantodonts (McGee and Turnbull 2010), equids (Hellmund 2013), and caprines (Jordana et al. 2013); others have found exceptions in different groups including lemurs (Godfrey et al. 2005; Schwartz et al. 2005), cercopithecines (Jogahara and Natori 2012), and tarsiids (Guthrie and Frost 2011).

## Phylogeny and Dental Eruption Patterns

Dental eruption in general has shown to be a reliable marker for relatedness among species. For Multituberculata, the rotative eruption of the fourth premolar, among other characters, has been proposed as synapomorphy for this group (Greenwald 1988). In the Hyaenodontidae, the different tooth eruption patterns between North American and European species have been interpreted as indicating phylogenetic signal (Bastl et al. 2011; Bastl and Nagel 2014). Afrotheria show a common synapomorphy in the development of their dentition; in general, the relative onset of the eruption of the permanent dentition is delayed compared to Archonta and Laurasiatheria (Asher and Lehmann 2008; Asher and Olbricht 2009). This is also found in xenarthrans, where the most basal forms seem to exhibit a relative delayed eruption of permanent dentitions (Ciancio et al. 2012). In primates, several studies have focused on the importance of phylogeny as explanation for differences in the tooth eruption sequence among species (Tattersall and Schwartz 1974; Byrd 1981; Schwartz et al. 2005).

## Material and Methods

### Specimens

A cross-sectional sampling of different ontogenetic stages of 452 cervid lower jaws representing 15 species was examined. Additionally, 30 lower jaws of *Moschus moschiferus* as well as 19 lower jaws of two tragulid species, *Hyemoschus aquaticus* and *Tragulus kaibabensis* (Institute and Museum der Univerchil), were examined (Table 1). The maximum number of lower jaws used per species was 146 (*Cervus elaphus*) and the minimum number was three (*Elaphodus cephalophus*). Captive as well as wild-caught animals of both sexes were used. Individuals exhibiting pathological signs in the lower jaw and domestic animals were excluded. Specimens from the following institutes have been studied: MHNG, Muséum d'Histoire Naturelle de la Ville de Genève; NMB, Naturhistorisches Museum Basel; NMBE, Naturhistorisches Museum Bern; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich; MfN, Museum für Naturkunde Berlin; ZMUZH, Zoologisches Museum der Universität Zürich; and ZSM, Zoologische Staatssammlung München. Further, we collected data from the literature

**Table 1** Tooth eruption sequences for investigated artiodactyl species

Family	Species	n	Pattern									
Cainotheriidae	<i>Caenomeryx filholi</i> <sup>a</sup>	66	m1	m2	i1	i2	i3	c	m3	p2	p3	p4
Cervidae	<i>Axis axis</i>	11	m1	m2	i1	i2	i3	c	m3	p4	p3	p2
	<i>Blastocerus dichotomus</i>	9	m1	m2	(i1	i2	m3)	i3	c	p4	p3	p2
	<i>Capreolus capreolus</i>	119	m1	m2	i1	i2	i3	m3	c	p2	p3	p4
	<i>Cervus elaphus</i>	146	m1	m2	i1	i2	m3	i3	c	p2	p3	p4
	<i>Cervus philisi</i> <sup>a</sup>	28	m1	(i2	m2)	m3	p3	p4	p2	-	-	-
	<i>Dama dama</i>	49	m1	i1	m2	i2	i3	c	m3	p4	p3	p2
	<i>Elaphodus cephalophus</i>	3	m1	m2	m3	i1	i2	i3	c	(p	p	p)
	<i>Eucladoceros giulii</i> <sup>a</sup>	60	m1	m2	m3	(p	p	p)	-	-	-	-
	<i>Heteroprox/Euprox</i> <sup>a</sup>	4	m1	m2	m3	(p	p	p)	-	-	-	-
	<i>Hippocamelus</i> sp.	4	m1	m2	m3	i1	i2	(p3	p4	p2	i3)	c
	<i>Hoplitomeryx</i> <sup>a</sup>	11	m1	m2	m3	(p	p	p)	-	-	-	-
	<i>Hydropotes inermis</i>	12	m1	m2	i1	i2	i3	c	m3	p4	p3	p2
	<i>Mazama gouazoubira</i>	34	m1	m2	m3	i1	i2	i3	c	p4	p3	p2
	<i>Muntiacus muntjak</i>	14	m1	m2	m3	i1	i2	p3	p2	p4	i3	c
	<i>Odocoileus virginianus</i>	12	m1	m2	i1	i2	i3	c	m3	(p	p	p)
	<i>Ozotoceros bezoarticus</i>	13	m1	m2	m3	i1	i2	i3	c	p4	p3	p2
	<i>Procervulus praelucidus</i> <sup>a</sup>	29	m1	m2	m3	(p	p	p)	-	-	-	-
	<i>Pseudodama s. l. nestii</i> <sup>a</sup>	20	m1	m2	m3	(p	p	p)	-	-	-	-
<i>Pudu puda</i>	12	m1	m2	m3	i1	i2	i3	c	(p	p	p)	
<i>Rusa timorensis</i>	5	m1	m2	i1	m3	i2	(i3	c	p4	p3	p2)	
<i>Rusa unicolor</i>	9	m1	m2	i1	i2	m3	i3	c	p4	p3	p2	
Tragulidae	<i>Hyemoschus aquaticus</i>	5	m1	m2	m3	i1	i2	i3	c	p4	p3	p2
	<i>Tragulus kanchil</i>	14	m1	m2	m3	(i1	p3	p4	p2)	i2	i3	c
Moschidae	<i>Moschus moschiferus</i>	30	m1	m2	m3	p4	p3	p2	i1	i2	i3	c

Unresolved sequences are indicated in parenthesis

<sup>a</sup> extinct

(Supplementary Table 1) to compare and analyze the correlations among variables studied.

Additionally, the tooth eruption patterns of seven extinct taxa were investigated: *Caenomeryx filholi*, *Pseudodama s. l. nestii*, *Eucladoceros giulii*, *Heteroprox/Euprox*, *Hoplitomeryx*, *Cervus philisi*, and *Procervulus praelucidus* (Table 1). *Heteroprox/Euprox* cannot be distinguished by dental characters and are treated as a unit. For fossil material, the following institutes were visited: IQW, Senckenberg Forschungsstation für Quartär-Paläontologie Weimar; NMB, Naturhistorisches Museum Basel; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie; and NBC, Naturalis Biodiversity Center.

**Data Collection**

The eruption sequence of the lower jaw was documented. Each tooth was coded as not erupted, erupting, or fully erupted/functional. Teeth that were already visible under the bone but had not begun to erupt were coded as 0. As

soon as one cusp or part of the tooth had penetrated through the bone it was coded as 1 and as soon as the tooth reached the functional position it was coded as 2. Nonetheless, due to different speeds of eruption, especially for the third molar, also the status of wear of the dentition and the height above the alveoli were taken into account for the sequences. Not represented stages were reconstructed according to anterior-posterior sequence as it holds true for incisors as well as molars.

**Phylogenetic Framework for Cervidae**

We used a compound tree based on different sources as phylogenetic framework for the heterochronic analysis. The main arrangement is according to the phylogeny of Gilbert et al. (2006). The position of *Ozotoceros bezoarticus* follows Barbanti Duarte et al. (2008) and *Candiacervus* sp. was placed as sister taxon of the fallow deer, *Dama dama* (de Vos 1984). Most branch lengths were taken from Gilbert et al. (2006). Additional branch lengths were taken from Barbanti Duarte et al. (2008) to include

*Ozotoceros bezoarticus* as well as the split of the two *Odocoileus* species. The divergence age for the split between the *Muntiacus* species was taken from Hernández Fernández and Vrba (2005). Splitting age between *Candiacervus* and *Dama* was estimated at around 2.15 Ma because the ancestor of *Dama dama* separated from the ancestor of *Cervus elaphus* and *Rusa unicolor* around 4.3 Ma ago (Gilbert et al. 2006).

### Heterochrony Analysis for Cervidae

The resolution of the sequences of eruption was completely resolved for 12 cervid species: *Axis axis*, *Capreolus capreolus*, *Cervus elaphus*, *Dama dama*, *Elaphodus cephalophus*, *Hydropotes inermis*, *Mazama gouazoubira*, *Muntiacus muntjak*, *Odocoileus virginianus*, *Ozotoceros bezoarticus*, *Pudu puda*, and *Rusa unicolor*. Four species were added to the analyses based on literature data: *Candiacervus* sp. (van der Geer et al. 2014), *Muntiacus reevesi* (Chapman et al. 1985), *Odocoileus hemionus* (Mosby 1960), and *Rangifer tarandus* (Miller 1972). Two different methods were used to infer the heterochronic shifts as well as the ancestral sequence of tooth eruption. One was a PGI - Parsimov-based genetic inference (Harrison and Larsson 2008). This method reconstructs sequence heterochronies as well as ancestral states by treating the whole sequence as one character and using a Parsimov-based algorithm for edit-cost optimization. The analysis was conducted using the R software (version 3.0.2) as well as the package *pgi* 2.0. Included in this analysis were 16 cervid species as well as the eruption of the ten teeth of the adult dentition. Eruption of premolars was coded as one single event due to the significant intraspecific variation of the eruption sequence of premolars in Cervidae. The following parameters were used to conduct eight different PGI-analyses: number of sequences per cycle: 150; number of cycles: 150; and number of sequences retained at each node: 150. The semi-exhaustive search was limited to 10,000 permutations per cycle. All eight analyses were performed independently and the shortest tree was chosen because it represents the most parsimonious scenario for heterochronic shifts. In addition to a PGI-analysis, a continuous analysis (Germain and Laurin 2009) was conducted, resulting in an ancestral sequence, heterochronic shifts, as well as a 95 % confidence interval. This analysis uses squared-change parsimony (Maddison 1991) and independent contrast (Felsenstein 1985), and it is based on a Brownian motion model. The different stages were standardized between 0 and 1 using adjusted ranks formula:

$$r_s = (r - r_{\min}) / (r_{\max} - r_{\min})$$

(Laurin and Germain 2011). Continuous analysis was performed using Mesquite (version 3.01) (Maddison and Maddison 2011), together with the module PDAP:PDTree (version 1.16) (Midford et al. 2011).

### Life History

Ruminant life history variables collected from the literature (Pérez-Barbería and Gordon 2005; Tacutu et al. 2013) include longevity, body weight, brain weight, weaning period, and the age of sexual maturity for females (Supplementary Table 2). Information on the age of first molar eruption was taken from different sources: *Apeyceros melampus* (Roettcher and Hofmann 1970), *Alces alces* (Peterson 1955), *Antidorcas marsupialis* (Rautenbach 1971), *Antilocapra americana* (Lubinski 2001), *Bison bonasus* (Wegrzyn and Serwatka 1984), *Capra ibex* (Habermehl 1985), *Capra pyrenaica* (Vigal and Machordom 1985), *Capreolus capreolus* (Habermehl 1985), *Capricornis crispus* (Miura and Yasui 1985), *Cervus elaphus* (Habermehl 1985), *Cervus nippon* (Ohtaishi 1980), *Connochaetes taurinus* (Attwell 1980), *Dama dama* (Habermehl 1985), *Damaliscus lunatus* (Mertens 1984), *Eudorcas thomsonii* (Robinette and Archer 1971), *Giraffa camelopardalis* (Hall-Martin 1976), *Hemitragus jemlahicus* (Caughley 1965), *Hippotragus niger* (Grobler 1980), *Muntiacus reevesi* (Chapman et al. 1985), *Odocoileus hemionus* (Mosby 1960), *Odocoileus virginianus* (Severinghaus 1949), *Oryx leucoryx* (Ancrenaz and Delhomme 1997), *Ovibos moschatus* (Henrichson and Grue 1980), *Ovis ammon* (Habermehl 1985), *Ovis canadensis* (Mosby 1960), *Ovis dalli* (Hemming 1969), *Ozotoceros bezoarticus* (Bianchini and Delupi 1993), *Rangifer tarandus* (Miller 1972), *Rupicapra pyrenaica* (Pérez-Barbería and Mutuberría 1996), *Rupicapra rupicapra* (Habermehl 1985), *Saiga tatarica* (Bannikov et al. 1961), *Sylvicapra grimmia* (Wilson et al. 1984), *Syncerus caffer* (Taylor 1988), and *Tragelaphus oryx* (Jeffery and Hanks 1981).

We investigated the relationship between hypsodonty index (Janis 1988) and permanent tooth eruption sequence as well as age of first molar eruption (Supplementary Table 2). First, the age of first molar eruption in the lower jaw was tested against the other variables. Second, the tooth eruption sequences of different ruminants were sorted into six different groups as predicted by Schultz's Rule. Groups are based on relative timing between tooth replacement and molar eruption (Table 2). Kendall's tau was used to test for statistical support for the correlations. Statistical analyses were performed in PAST software (version 2.17c) (Hammer et al. 2001). Adobe Photoshop CS5 was used to create the artwork for this study.

## Results

### Tooth Eruption

The recorded eruption sequences are shown in Table 1. Not all relative sequences could be documented to completion. All investigated Cervidae start the eruption sequence with the first

**Table 2** Grouping of the tooth eruption sequences according to the Schultz’s Rule

Group	Eruption sequence	Species
1	<b>m1 m2 m3</b> (i1 i2 i3 c p2 p3 p4)	<i>Antidorcas marsupialis</i> , <i>Antilocapra americana</i> , <i>Elaphodus cephalophus</i> , <i>Eudorcas thomsonii</i> , <i>Giraffa camelopardalis</i> , <i>Hippotragus niger</i> , <i>Hyemoschus aquaticus</i> , <i>Mazama gouazoubira</i> , <i>Moschus moschiferus</i> , <i>Muntiacus muntjak</i> , <i>Muntiacus reevesi</i> , <i>Ozotoceros bezoarticus</i> , <i>Pudu puda</i> , <i>Saiga tatarica</i> , <i>Sylvicapra grimmia</i> , <i>Syncerus caffer</i>
2	<b>m1 m2</b> (i1 <b>m3</b> i2 i3 c p2 p3 p4)	<i>Aepyceros melampus</i> , <i>Capricornis crispus</i> , <i>Connochaetes taurinus</i> , <i>Damaliscus lunatus</i> , <i>Rusa timorensis</i> , <i>Rupicapra pyrenaica</i> , <i>Oreamnos americanus</i> , <i>Oryx leucoryx</i> , <i>Ovibos moschatus</i> , <i>Ovis dalli</i> , <i>Tragelaphus oryx</i>
3	<b>m1 m2</b> (i1 i2 <b>m3</b> i3 c p2 p3 p4)	<i>Capra ibex</i> , <i>Cervus elaphus</i> , <i>Rusa unicolor</i>
4	<b>m1 m2</b> (i1 i2 i3 <b>m3</b> c p2 p3 p4)	<i>Capreolus capreolus</i>
5	<b>m1 m2</b> (i1 i2 i3 c <b>m3</b> p2 p3 p4)	<i>Axis axis</i> , <i>Hydropotes inermis</i> , <i>Odocoileus hemionus</i> , <i>Odocoileus virginianus</i>
6	<b>m1</b> (i1 <b>m2</b> i2 i3 c <b>m3</b> p2 p3 p4)	<i>Candiacervus</i> sp., <i>Dama dama</i> , <i>Rangifer tarandus</i>

Molars are in bold and replacement teeth are unordered (indicated by parenthesis)

molar, and except for the genera *Muntiacus* and *Hippocamelus*, all end the sequence with the eruption of the premolar teeth. In *Hippocamelus* sp. and *Muntiacus muntjak*, as well as in ruminants *Moschus moschiferus* and *Tragulus kanchil*, the last tooth to erupt was the canine. Premolar teeth always erupted simultaneously or closely tight in timing. In all South American cervids, the molar eruption took place before the first incisors were replaced. The only exception might be *Blastocerus dichotomus*, but the relative eruption sequence of i1 – i2 – m3 could not be resolved. Other related species with the same sequence are *Candiacervus* sp. and *Dama dama* with m1 – i1 – m2 – i2 – i3 – c – m3 – p4 – p3 – p2 (van der Geer et al. 2014) as well as both *Odocoileus* species also with m1 – m2 – i1 – i2 – i3 – c – m3 – (p – p – p) (Mosby 1960). The *Odocoileus virginianus* sequence differs from the ones described by Severinghaus (1949) and Brokx (1972). Three different premolar sequences were recorded in *Capreolus capreolus* (Table 3). The relative position of the third molar is not stable; it can erupt either before the third incisor or before or after the canine. *Cervus elaphus* is the most variable species, with four different tooth eruption sequences and the only documented case where premolar eruption preceded third molar eruption in one case (Table 4). The most common sequence, however, is m1 – m2 – i1 – i2 – m3 – i3 – c – p2 – p3 – p4. The closely related *Rusa* species do not share a common replacement pattern. *Rusa unicolor* replaces the teeth in the order of m1 – m2 – i1 – i2 – m3 – i3 – c – (p4 – p3 – p2), whereas *Rusa timorensis* replaces in a different order: m1 – m2 – i1 – m3 – i2 – (i3 – c – p4 – p3 – p2). Although the final sequence could not conclusively be resolved, the third molar has accelerated its eruption before the second incisor in *Rusa timorensis*.

In addition to the cervid species, the permanent tooth eruption pattern of one moschid species and two tragulid species were documented. Most basal of these are the tragulids *Hyemoschus aquaticus* and *Tragulus kanchil*. For *Hyemoschus aquaticus*, the sequence is m1 – m2 – m3 – i1

– i2 – i3 – c – p4 – p3 – p2 and for *Tragulus kanchil*, m1 – m2 – m3 – (i1 – p3 – p4 – p2) – i2 – i3 – c. The resolution of the incisors is based on the constant anterior-posterior replacement of these teeth, a pattern that rarely changes. In these two species the permanent tooth eruption patterns differ. While in one tragulid species, *Tragulus kanchil*, the eruption of the replacement teeth is premolars before incisors (with overlap), in *Hyemoschus aquaticus* a replacement pattern from anterior to posterior can be found. In *Moschus moschiferus*, the sequence is m1 – m2 – m3 – p4 – p3 – p2 – i1 – i2 – i3 – c, comparable to the one from *Tragulus kanchil*, and not documented in any cervid species. The bovid, *Sylvicapra grimmia* has a comparable tooth eruption sequence (Wilson et al. 1984).

### Heterochrony

The PGI analyses resulted in eight consensus trees of similar length (minimum tree length: 9). This overall consensus in tree length suggests a very stable analysis and a fitting use of parameters. The resulting ancestral sequence for Cervidae is m1 – m2 – i1 – i2 – i3 – c – m3 – (ppp). This sequence is still present or common in *Axis*, *Odocoileus*, *Capreolus*, *Hydropotes*, and also within the range of variation of *Cervus elaphus*. Most changes happened in the sequence of the genus *Muntiacus*. Here, the analysis resulted in an acceleration of the third molar for the genera *Muntiacus* and *Elaphodus* (Muntiacini) and also in delayed eruption of the third incisor and the canine for *Muntiacus*. The uniform tooth eruption sequence of the South American representatives in the dataset originates from an accelerated eruption of the third molar. In general, cervids accelerate the eruption of different tooth positions rather than delay eruption. Details about the heterochronic shifts in the eruption sequence of cervids in phylogeny based on PGI-analysis are depicted in Fig. 1.

The continuous method resulted in an ancestral sequence of m1 – m2 – i1 – i2 – m3 – i3 – c – (ppp). This sequence was

**Table 3** Variation in permanent premolar tooth eruption sequence found in this study

		n	p2 - p3 - p4	p4 - p3 - p2	p3 - p2 - p4	p3 - p4 - p2	(p2 - p4) - p3
Cainotheriidae	<i>Caenomeryx filholi</i> <sup>a</sup>	3	2	–	1	–	–
Cervidae	<i>Axis axis</i>	1	–	1?	–	–	–
	<i>Blastocerus dichotomus</i>	2	–	2	–	–	–
	<i>Capreolus capreolus</i>	10	6	3	–	–	1
	<i>Cervus elaphus</i>	5	4	1	–	–	–
	<i>Cervus philisi</i> <sup>a</sup>	2	–	–	–	2	–
	<i>Dama dama</i>	2	–	2	–	–	–
	<i>Hippocamelus</i> sp.	2	–	–	–	2	–
	<i>Hydropotes inermis</i>	2	–	2	–	–	–
	<i>Mazama gouazoubira</i>	1	–	1	–	–	–
	<i>Muntiacus muntjak</i>	2	–	–	2	–	–
	<i>Ozotocerus bezoarticus</i>	2	–	2	–	–	–
	<i>Rusa timorensis</i>	2	–	2	–	–	–
	<i>Rusa unicolor</i>	1	–	1?	–	–	–
Moschidae	<i>Moschus moschiferus</i>	1	–	1	–	–	–
Tragulidae	<i>Hyemoschus aquaticus</i>	1	–	1	–	–	–
	<i>Tragulus kanchil</i>	1	–	–	–	1	–

<sup>a</sup> extinct

documented in *Cervus elaphus* as well as *Rusa timorensis*. In general, the continuous method resulted in more heterochronic shifts than the PGi-analysis. All represented species had a heterochronic shift in the second lower incisor, mostly accelerating its eruption (Fig. 2).

### Life History

In the investigated ruminants the age of first molar eruption as well as the pattern of dental eruption were compared with each other as well as with life history and anatomical variables. When comparing the time of first molar eruption with the grouped tooth eruption sequences, no significant correlation was detected using Kendall's tau. Nonetheless, the trend was positive. The size of the brain was highly correlated with the

age of first molar eruption but not with the emergence pattern itself. However, it showed a positive trend for both correlations. Weight showed a positive correlation with the age of first molar eruption but not with the pattern of permanent tooth emergence. Longevity was also highly correlated with the age of first molar eruption and showed a positive trend. It was not correlated with the pattern of tooth eruption. The same is true for the age of female sexual maturity and weaning period. No significant correlation was found between the hypsodonty index and the pattern of permanent tooth emergence (Table 5).

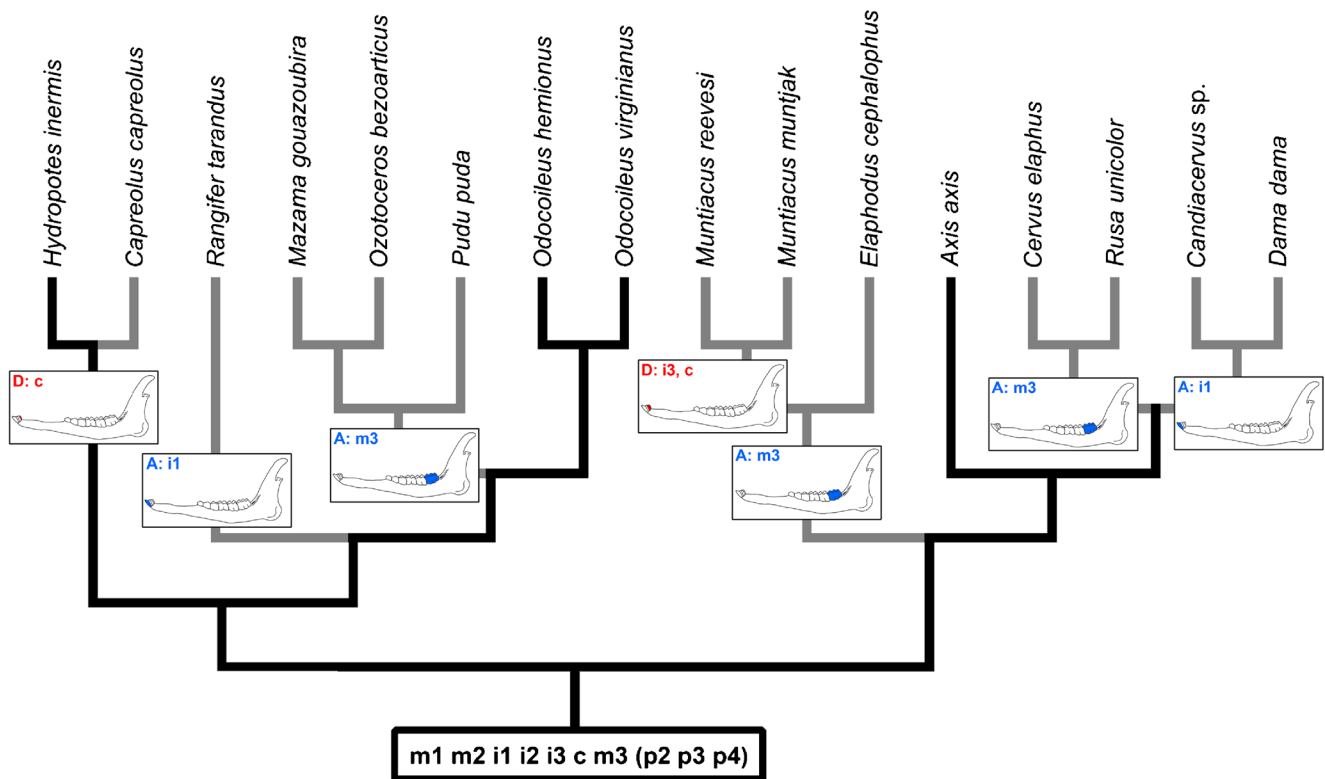
### Discussion

This study aimed at investigating the tooth eruption sequence in Cervidae and at demarcating impacting factors thereof. Altogether, 16 lower jaw eruption sequences of cervids were used to infer the ancestral stage of tooth eruption as well as heterochronic shifts. *Cainotherium filholi* exhibited the same relative eruption sequence of the permanent dentition as the inferred ancestral stage for cervids from the PGi-analysis.

Our analyses show that the eruption patterns in ruminants are not significantly influenced by life history variables or hypsodonty. In general, related species tend to share a common or similar eruption pattern. In cervids, the overall variability of the eruption patterns is restricted due to anatomical constraints such as the ability of the jaw to accommodate all molars and the close timing of eruption of the three premolar teeth.

**Table 4** Variation of permanent tooth emergence sequences found in this study

<i>Cervus elaphus</i>							
m1	m2	i1	i2	i3	c	(ppp)	
m3							
<i>Capreolus capreolus</i>							
m1	m2	i1	i2	i3	c	(ppp)	
m3							
<i>Muntiacus muntjak</i>							
m1	m2	m3	i1	i2	i3	c	(ppp)



**Fig. 1** Result of the sequence heterochrony analysis using PGI (Harrison and Larsson 2008). The reconstructed ancestral eruption sequence for the lower jaw is listed at the root and species and reconstructed lineages exhibiting this eruption sequence are traced in black. Grey lines indicate

a change of this pattern. Lower jaws show the sequential change for a grey line and the affected tooth position. red: tooth position erupts delayed, blue: tooth position erupts accelerated

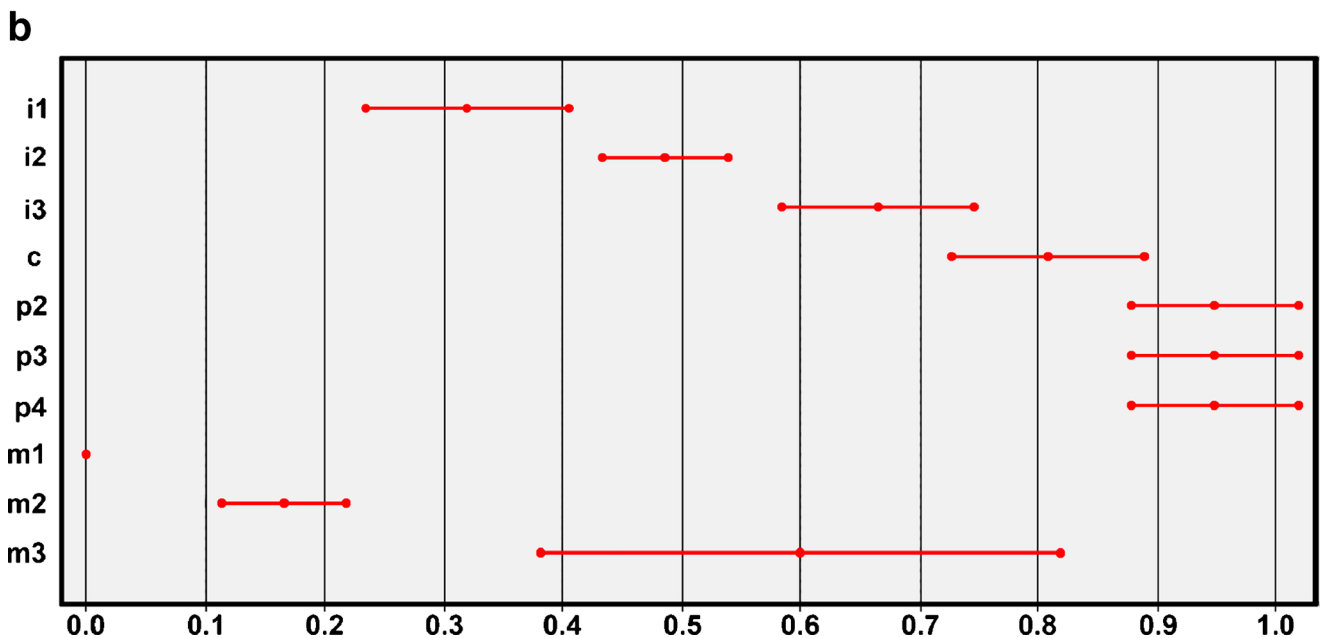
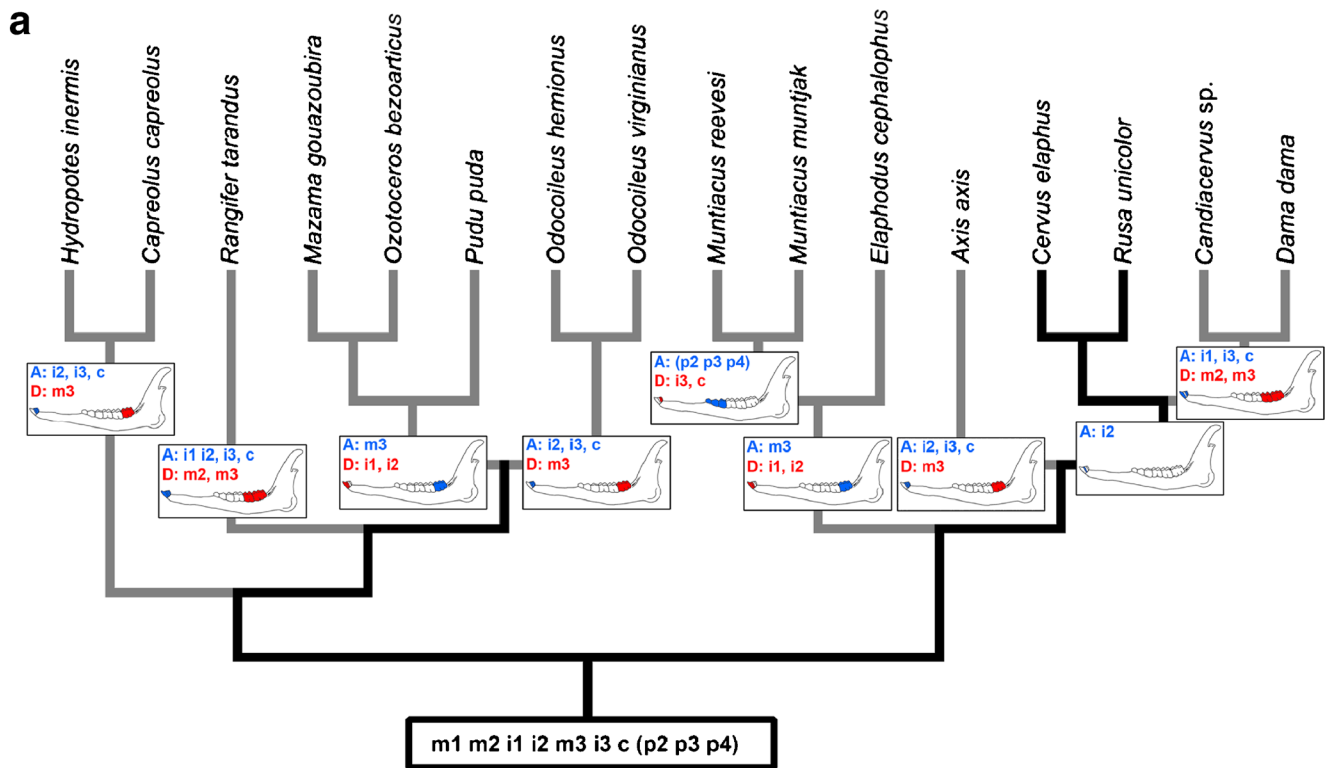
### Sequence of Replacement

In cervids, incisors are replaced sequentially from anterior to posterior. This is also the case in all examined moschids, tragulids, *Camelus* (Bello et al. 2013), and all documented ruminants from the literature. The lower canine in Ruminantia is incisiviform and increases the size of the incisor shovel (e.g., Thenius 1989). Usually, this tooth is replaced after i3 and therefore follows the anterior-posterior sequential replacement, although eruption of i3 and canine can be closely timed (e.g., Severinghaus 1949; Habermehl 1985; Ancrenaz and Delhomme 1997). The anterior-posterior eruption sequence of the incisors and canines, however, is not generally fixed in placentals (e.g., Kirkpatrick and Sowls 1962; Matschke 1967; Smuts 1974; Habermehl 1975; Smuts et al. 1978; Shigehara 1980; Smith 2000; van Horn et al. 2003; Asher and Olbricht 2009).

The premolar teeth are replaced more or less simultaneously in cervids and any tooth could start the eruption sequence. This is supported by lower jaws where premolar height above the alveoli suggests simultaneous eruption. For *Rangifer tarandus* and *Odocoileus virginianus*, a sequence of (p2 – p3) – p4 or p2 – (p3 – p4) has been postulated (Miller 1972; Severinghaus 1949) and for *Odocoileus hemionus* a sequence

of p3 – p4 – p2 (Robinette et al. 1957). Van der Geer et al. (2014) proposed a posterior-anterior replacement pattern for the premolar eruption sequence for *Candiacevus*. Habermehl (1985) documented an alternate replacement for the roe deer with p3 – p2 – p4. In Bovidae, the premolar eruption pattern is not fixed either. Nonetheless, in many species a pattern of p2 – p3 – p4 has been postulated, although for some the p2 is missing (Supplementary Table 1). Here, no case of reversed sequence has been reported but alternate eruption, either (p3 – p4) – p2 (Mosby 1960; Hemming 1969; Vigal and Machordom 1985) or p3 – (p2 – p4) (Caughley 1965). It has been widely accepted that ruminants share a sequential pattern (p2 – p3 – p4 or p4 – p3 – p2) of replacing teeth usually in the order of p2 – p3 – p4 (Osborn 1970; Smith 2000; Luo et al. 2004), but data presented here show that premolar eruption sequence can vary even in closely related species or within a species. This is also true in other placentals, although premolar eruption might not be as closely timed as in cervids (Slaughter et al. 1974; Tattersall and Schwartz 1974; Smith 1994, 2000; Gingerich and Smith 2010).

Molar eruption in cervids occurs in all recorded cases from anterior to posterior, with no exception. No evidence from other placentals has been found to contradict this (e.g., Slaughter et al. 1974; Habermehl 1985; Smith 2000).



**Fig. 2** Result of the sequence heterochrony analysis using continuous analysis (Germain and Laurin 2009). **a** The reconstructed ancestral eruption sequence for the lower jaw is listed at the root and reconstructed lineages exhibiting this eruption sequence are traced in black. Grey lines indicate a heterochronic shift in this pattern. Lower

jaws indicate the sequential change for a line and the affected tooth position. red: tooth position erupts delayed, blue: tooth position erupts accelerated. **b** 95 % confidence intervals for every single tooth position. The ancestral eruption sequence is represented as midpoint and with extreme points the 95 % confidence intervals are shown

**On the Methods of Sequence Heterochrony Analysis**

We found differences in the results between PGi-analysis and continuous analysis, as was the case in several other studies

(Geiger et al. 2014; Koyabu et al. 2014; Sheil et al. 2014). This is due to the different approach both methods have. PGi-analysis is not based on a time tree and it can deal with ties or simultaneous events in the dataset (Harrison and Larsson



**Table 5** P-values from Kendall's tau for different life history traits as well as for hypsodonty index

		m1	Longevity	Brain mass	Body mass	Sexual maturity (f)	Weaning period	Hypsodonty index
m1	p-value:	–	0.005*	0.001*	<0.001*	<0.001*	0.007*	0.325
	tau:	–	0.347	0.466	0.513	0.412	0.363	0.132
Emergence Pattern	p-value:	0.186	0.393	0.093	0.053	0.115	0.427	0.318
	tau:	0.185	0.098	0.221	0.219	0.183	0.102	–0.129

It was tested for the time of first molar eruption (months) as well as for the emergence pattern itself grouped according to Table 2

2008). On the other hand, the continuous analysis incorporates branch length data and can be biased due to unresolved sequences (Germain and Laurin 2009; Koyabu et al. 2014). The transformation of the data can also be a source of bias as transformed data have the same intervals between events (Germain and Laurin 2009). Both methods differ in dealing with independence in the dataset. PGI-analysis does not assume independence between events (Harrison and Larsson 2008); continuous analysis, on the other hand, does (Germain and Laurin 2009). In general, the continuous analysis resulted in more heterochronic shifts than the PGI-analysis. Nonetheless, the 95 % confidence interval of the continuous analysis supports the result of the PGI-analysis.

### Morphological Constraints, Adaption, and Dental Eruption Patterns

Simpson et al. (1990) hypothesized that the pattern of eruption of permanent dentition can be influenced by the anatomy of the upper or lower jaw. Certain anatomical constraints are also part of Schultz's Rule (Smith 2000). Cervids and bovids share a very similar dentary shape as well as tooth formula with the four anterior incisiviform teeth followed by a diastema and afterwards three premolars and three molars (e.g., Thenius 1989). Nonetheless, they do not all share the same pattern of tooth replacement. Whereas, e.g., *Dama dama* and *Candiacervus* start to replace their first incisor already early, *Pudu puda* and *Mazama gouazoubira* replace this tooth after the eruption of all three molars. The stable pattern in the cheek-dentition in cervids, where premolar teeth nearly always erupt after the third molar, indicates that replacement occurs as soon as the mandible is big enough to accommodate the whole permanent dentition. This holds also for *Hyemoschus aquaticus*, *Tragulus kanchil*, and *Moschus moschiferus*. In rare cases (once in *Cervus elaphus*), the premolar eruption precedes third molar eruption. Only a few Ruminantia such as *Ovis ammon* (Habermehl 1985) and *Myotragus balearicus* (Jordana et al. 2013) change the relative sequence between premolar eruption and the third molar one completely.

A simple but effective way to account for the effect of morphology in the ruminant dentition is the hypsodonty index

(Janis 1988). Ruminant teeth share general tooth morphology; all are selenodont (e.g., Thenius 1989; Hillson 2005). Not all teeth, however, have the same height and therefore not all teeth need the same space within the jaw. Using Kendall's tau to analyze the relation between the pattern of tooth emergence and the age of first molar eruption did not result in a correlation between these parameters (Table 5). Although the size of the crown height is definitely different among the species examined, it did not lead to a change in relative eruption sequence. High crowned species such as *Antidorcas marsupialis* or *Eudorcas thomsonii* have the same eruption sequence as the low crowned *Hyemoschus aquaticus* or *Elaphodus cephalophus*. Hypsodonty does not influence the relative emergence pattern of the permanent dentition in ruminants.

### Tooth Eruption as Indicator for Life History Traits

The time of eruption of the first molar was positively correlated with longevity, age of female sexual maturity, brain mass, weaning period, and body mass. For primates and "ungulates," positive correlations among some of these traits have also been found, although not always significant (e.g., Smith 1989, 1992, 2000; Godfrey et al. 2001, 2005; Guthrie and Frost 2011). A link among different life history traits in general has been found in Artiodactyla. Brain size, for example, is correlated with body mass, and body mass again is correlated with maximum longevity (Isler and van Schaik 2012). Body size in a broad sense can be a predictor for the pace of life history. However, it might not be the source of differences (e.g., Western 1979; Read and Harvey 1989). Therefore, the age of first molar eruption can be seen as a predictor for the pace of life history in the investigated ruminants. The pattern of eruption is not linked to these life history and anatomical traits (Table 5). Schultz's Rule fails to predict the life history of Ruminantia in this case. An outstanding example in this regard is the emergence sequence of the two taxa *Muntiacus* and *Giraffa*. Both genera share the same tooth eruption pattern, but all life history variables investigated differ considerably. For example, the age of first molar eruption is 10 months in *Giraffa camelopardalis* but only 0.23 months in *Muntiacus reevesi* (Supplementary Table 2).

## Phylogeny and Dental Eruption Patterns

The tooth eruption sequence in cervids, as in other mammals, is largely conserved in phylogeny (e.g., Byrd 1981; Greenwald 1988; Luo et al. 2004; Asher and Lehmann 2008; Ciancio et al. 2012), as for example seen in the genera *Capreolus* and *Hydropotes* as well as *Muntiacus* and *Elaphodus*. The divergence splits of both groups have been estimated with around 7.3 Ma for Muntiacini and 5.6 Ma for Capreolini (Gilbert et al. 2006). Nonetheless, *Capreolus* still shows the eruption sequence of *Hydropotes* within its variability, and within Muntiacini, the eruption pattern of *Elaphodus cephalophus* falls within the range of variation of *Muntiacus muntjak* (Table 4). Other examined taxa also have similar eruption sequences such as *Pudu puda*, *Mazama gouazoubira*, and *Ozotoceros bezoarticus*; *Dama dama* and *Candiacervus* sp.; as well as *Rusa unicolor* and *Cervus elaphus* (Table 1). The genus *Odocoileus* is more variable than is recorded in this study. Patterns from literature differ from the pattern observed here. *Odocoileus virginianus* for example has been documented with the same tooth eruption sequence as *Rangifer tarandus* (Severinghaus 1949; Miller 1972).

In Bovidae, some closely related species have similar sequences such as *Ovibos* and *Capricornis* as well as *Eudorcas* and *Antidorcas* (Supplementary Table 1). The emergence patterns of bovids in general, however, are less well resolved and many species exhibit unique eruption patterns. An explanation for this might be that the taxa represented are usually not closely related, having divergence times of more than 5–10 Ma (Bibi 2013).

## Comparisons with Fossil Artiodactyls

One extinct taxon studied preserved a complete permanent eruption pattern in the lower jaw, the caenotherid *Caenomeryx filholi*, from the Oligocene of Gaimersheim (Fig. 3). Cainotheriidae are a sister taxon to ruminants (Theodor 2010). The sequence represented in this artiodactyl is in concordance with the result of the PGi-analysis (Fig. 1). Lower first premolars have been lost in modern ruminants (Thenius 1989). *Caenomeryx filholi* still possesses the complete ancestral tooth formula 3143/3143 of placental mammals (Thenius 1989) and therefore preservation of ancestral characteristics in replacement order of permanent teeth is possible.

All examined fossils from extinct taxa in this study have a constant pattern in premolar-molar eruption. This persistence

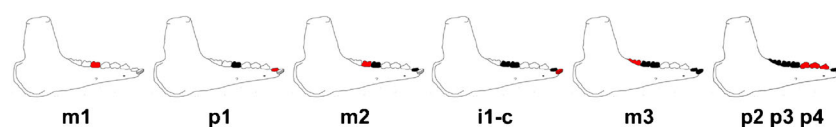
of premolar eruption after molar eruption stands in contrast to Schultz's Rule, because body size range, a proxy for life history, among these species is large (e.g., Western 1979; Read and Harvey 1989).

From the literature, the ruminant *Myotragus balearicus* follows Schultz's Rule scenario (Jordana et al. 2013). This extinct island bovid has an eruption sequence of  $m1 - i1 - m2 - (p3 - p4) - m3$  and the first molar emerged at around nine months (Jordana et al. 2013). It is one of the rare cases where premolar eruption accelerated the third molar one and studies showed that this species had a slow life history as well as a long life span (Marín-Moratalla et al. 2011; Jordana et al. 2012, 2013). The next living relative to the genus *Myotragus*, however, is the genus *Ovis* (Lalueza-Fox et al. 2005). *Ovis ammon* also accelerates premolar eruption before the third molar one (Habermehl 1985). Therefore, the eruption pattern of *Myotragus* might be influenced by phylogeny as well.

## Conclusion

Tooth eruption in cervids, as commonly in extant Ruminantia, shows that there is variation in the permanent tooth eruption sequences even among closely related species. According to our results, these sequential differences are not influenced by brain size, body mass, hypsodonty, or the life history factors tested for but rather by their phylogeny. Closely related species often share their tooth eruption sequences and differences in patterns can be explained by observed intraspecific and interspecific variations. These results stand in contrast to the proposed Schultz's Rule-hypothesis because here, the speed of growth should have had a bigger impact on the permanent tooth eruption sequence than any other factor (Smith 2000). Nonetheless, Smith (2000) stated that the predictions of this rule are not as strong for ruminant artiodactyls, which she included in so called "specialized ungulates." These "ungulates" would only slowly adapt to changes in pace of life history.

The age of first molar eruption, however, was correlated with life history variables such as longevity, age of female sexual maturity, and weaning period. Both brain weight and weight in general were highly correlated with age of first molar eruption. This agrees with the literature on primates as well as "ungulates" (e.g., Smith 1989, 2000; Smith et al. 1994; Godfrey et al. 2001, 2005; Guthrie and Frost 2011). The fossil record as well as heterochrony methods allow for reconstruction of the ancestral emergence pattern. A pattern of  $m1 - m2$



**Fig. 3** Documented tooth eruption sequence for the lower jaw of *Caenomeryx filholi*. Newly erupted teeth (red), previously erupted ones (black)

–i1 – i2 – i3 – c – m3 – (ppp) holds true for the common ancestor of today's cervids, based on results from PGI-analysis, as well as for *Caenomeryx filholi*.

Premolar eruption remains unresolved due to the variability of relative eruption sequence in these teeth. Sequential as well as alternate replacement was documented even within one species, which makes phylogenetic statements based on premolar replacement problematic.

**Acknowledgments** We thank the following colleagues for access to collections: Loïc Costeur (NMB), Christiane Funk (MfN), Alexandra van der Geer (NBC), Marianne Haffner (ZMUZH\_MAMM), Stefan T. Hertwig (NMBE), Michael Hiermeier (ZSM), Lars van den Hoek Ostende (NBC), Ralf-Dietrich Kahlke (IQW), Barbara Oberholzer (ZMUZH\_MAMM), Itatí A. Olivares (MLPA), Gertrud Rössner (BSPG), Manuel Ruedi (MHNG), Manuel Schweizer (NMBE), and Diego H. Verzi (MLPA). Our gratitude goes also to Madeleine Geiger (PIMUZ), Robert Asher (UMZC), Daisuke Koyabu (UMUTZ), and the anonymous reviewer for their helpful advice with methodological questions as well as for discussion and to Ashley Latimer (PIMUZ) for reviewing the English. This research was funded by the Swiss National Science Foundation (SNF) grant 31003A\_149605 to Marcelo R. Sánchez-Villagra.

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