

UC Berkeley

UC Berkeley Electronic Theses and Dissertations

Title

On the Sequence of Postcanine Tooth Eruption in Mammals

Permalink

<https://escholarship.org/uc/item/0f53861c>

Author

Monson, Tesla Allyse

Publication Date

2017

Peer reviewed|Thesis/dissertation

On the Sequence of Postcanine Tooth Eruption in Mammals

By

Tesla Allyse Monson

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Dr. Leslea Hlusko, Chair

Dr. Charles Marshall

Dr. Jun Sunseri

Spring 2017

On the Sequence of Postcanine Tooth Eruption in Mammals

Copyright © 2017
by
Tesla Allyse Monson

Abstract

On the Sequence of Postcanine Tooth Eruption in Mammals

by

Tesla Allyse Monson

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Dr. Leslea Hlusko, Chair

As the key physical interface between mammals and their environment, teeth are extremely important biological structures and a great deal is known about the biology of tooth eruption. Nonetheless, there remains significant disagreement on whether life history, phylogeny, or possibly other factors, are driving the evolution of dental eruption sequence in mammals. Schultz's Rule, which states that eruption sequence is adaptive and associated with life history variables like postnatal growth and longevity, has also been used in dozens of studies of extant and fossil mammals since it was proposed by Smith in 2000. However, none of these studies account for phylogeny in their analyses.

To address this, I assessed postcanine dental eruption sequence across a large sample of primates and artiodactyls in order to test two hypotheses: 1) dental eruption sequence is associated with life history variables like post-natal growth and longevity in mammals (Schultz's Rule), and as such could be adaptive, and 2) eruption sequence is a good phylogenetic character for primates and artiodactyls. I examined the dentition of more than 8,000 animals and assessed postcanine eruption sequence in 31 primate and 81 terrestrial artiodactyl genera, spanning 10 families in each clade. With the inclusion of 30 additional primate genera from the literature, this is the most comprehensive compilation of dental eruption sequence in mammals to date.

Tests of phylogenetic signal show that dental eruption sequence is phylogenetically conserved in primates and artiodactyls as are almost all of the life history and body size traits tested here. However, only body size in primates is significantly associated with dental eruption sequence. Ancestral state reconstruction supports that the third molar erupted before one or more of the premolars in the ancestor of primates, while the third molar erupted after the premolars in the ancestor of artiodactyls. More derived clades within primates and artiodactyls have a different eruption sequence, where the third molar erupts after the premolars in anthropoids (Primates), and the third molar erupts before one or more of the premolars in Ruminantia (Artiodactyla). This change likely occurred during the Paleogene in both primates and artiodactyls. Within primates and artiodactyls, several taxa exhibit a dental eruption sequence that is either secondarily derived or a reversal to the ancestral state, and several taxa exhibit intra- and intraspecific variation in dental eruption sequence. Many of these secondary changes likely occurred in the Miocene and Pliocene. Dental eruption sequence is phylogenetically conserved in primates and artiodactyls, and changes in eruption sequence may be associated with

changes in body size. Variation in dental eruption sequence may also be related to the biomechanics of chewing. In both primates and artiodactyls, a fused mandible is associated with taxa that erupt the third molar after the premolars, while an unfused mandible is associated with taxa that erupt the third molar before one or more of the premolars. The evolution of symphyseal fusion of the mandible is convergent in several mammalian taxa, and in primates, mandibular fusion is thought to be an adaptation to the increasing mechanical stress associated with increasing body size in herbivorous animals.

The data in this study suggest that dental eruption sequence is likely driven by factors that include body size, fusion of the mandibular symphysis, and the biomechanics of chewing. It also seems likely that limited resource availability, as is seen in the island fossil caprine *Myotragus* and other extant high elevation caprines, can further affect the timing and sequence of dental eruption. Overall, Schultz's Rule, as it is currently written and applied, is not supported by this extended data set. Dental eruption sequence is phylogenetically conserved and is not associated with age at eruption of the first molar, longevity, or many other life history and size traits, with the exception of body size. Phylogeny, not life history, explains dental eruption sequence in mammals. My research demonstrates that dental eruption sequence is a far better predictor of phylogeny, and it will likely prove useful in phylogenetic hypotheses about relationships between extinct and extant mammalian taxa.

“There can be little doubt...”

Adolf Schultz, 1935

I hope there is always room for doubt.

Table of Contents

Dedication	i
Table of Contents	ii
List of Tables	vi
List of Figures	ix
List of Appendices	x
Acknowledgments	xi
CHAPTER 1: Mammalian dental eruption sequence	1
1.1 Overview	1
1.2 Evolution of the dentition	1
1.3 Dental eruption sequence	1
1.3.1 Schultz's study of dental eruption sequence	2
1.3.2 Hypotheses on the relationship between dental eruption sequence and phylogeny	3
1.4 Research questions and hypotheses	4
1.5 Dissertation overview	5
CHAPTER 2: Materials used in the assessment of dental eruption sequence	6
2.1 Overview	6
2.2 Evolution of the primates	6
2.2.1 The earliest primates	6
2.2.2 Evolution of the tarsiiiformes	7
2.2.3 Evolution of the anthropoids	7
2.2.4 Evolution of the strepsirrhines	8
2.3 Description of the primate sample	8
2.4 Evolution of the artiodactyls	18
2.4.1 The earliest artiodactyls	18
2.4.2 Domestication of artiodactyls	18
2.5 Description of the artiodactyl sample	18
2.6 Summary of the sample used in this study	23
CHAPTER 3: Survey of dental eruption sequence in extant primates and artiodactyls	24
3.1 Overview	24
3.2 Methods of assessing dental eruption sequence	24
3.3 Dental eruption sequences in primates	28
3.3.1 Atypical dental eruption sequences in haplorhines	28
3.3.1.A <i>Semnopithecus</i>	28
3.3.1.B <i>Aotus</i>	29
3.3.1.C <i>Pithecia</i>	29
3.3.2 Atypical dental eruption sequences in strepsirrhines	30
3.3.2.A Lemuriformes	30

3.3.3 Test of intraspecific variation in dental eruption sequence	30
3.3.4 Intraspecific variation in primate dental eruption sequence	31
3.3.4.A <i>Alouatta</i>	31
3.3.4.B <i>Callimico</i>	32
3.3.4.C <i>Saimiri</i>	32
3.3.4.D <i>Presbytis</i>	32
3.3.5 Summary of primate dental eruption sequences	33
3.4 Dental eruption sequence in artiodactyls	55
3.4.1 Variation in dental eruption sequence across artiodactyls	55
3.4.1.A Caprinae	55
3.4.1.B Simultaneous eruption of the fourth premolar and third molar in artiodactyls	56
3.4.2 Test of intraspecific variation in dental eruption sequence	56
3.4.3 Summary of artiodactyl dental eruption sequences	57
3.5 Summary of primate and artiodactyl dental eruption sequences	73
CHAPTER 4: Phylogeny, life history, and body size	74
4.1 Overview	74
4.2 Methods of generating phylogenies	74
4.3 Life history and body size variables	75
4.4 Phylogenetic independent contrasts between dental eruption sequence, life history, and body size	80
4.5 Results of the phylogenetic independent contrasts	80
4.5.1 Results for primates	80
4.5.2 Results for artiodactyls	81
4.6 Tests of phylogenetic signal	83
4.7 Results of the tests of phylogenetic signal	83
4.7.1 Results for primates	83
4.7.2 Results for artiodactyls	84
4.8 Summary of the phylogenetic tests	85
CHAPTER 5: Ancestral state reconstruction of dental eruption sequence in primates and artiodactyls	86
5.1 Overview	86
5.2 Ancestral state reconstruction	86
5.2.1 Taxonomic debates	86
5.3 Results of the maximum likelihood analysis in primates	87
5.3.1 Strepsirrhines	87
5.3.2 Tarsiiformes	87
5.3.3 Platyrrhines	87
5.3.4 Colobines	88
5.4 Results of the parsimony analysis in primates	88
5.5 Results of the maximum likelihood analysis in artiodactyls	92
5.5.1 Basal artiodactyls	92

5.5.2 Ruminants	92
5.5.3 Caprines	92
5.6 Results of the parsimony analysis in artiodactyls	93
5.7 Summary of the ancestral state reconstruction	97
CHAPTER 6: Incorporating the fossil record into our understanding of the evolution of dental eruption sequence in mammals	98
6.1 Overview	98
6.2 Dental eruption sequence in fossil primates	98
6.2.1 The earliest primates	98
6.2.2 Early anthropoids	98
6.2.3 Cercopithecoidea	99
6.2.4 Platyrrhines	101
6.2.5 Hominoids	101
6.2.6 Lemuriformes	101
6.3 Dental eruption sequence in fossil artiodactyls	106
6.3.1 Suina	106
6.3.2 Giraffidae	106
6.3.3 Hippopotamidae	107
6.3.4 <i>Diplobune</i> †	107
6.3.5 Caprinae	107
6.4 Summary of fossil primate and artiodactyl dental eruption sequences	108
CHAPTER 7: Discussion	110
7.1 Overview	110
7.2 Hypotheses about the drivers of dental eruption sequence in mammals	110
7.2.1 Body size	111
7.2.2 Resource availability and high-elevation habitats	112
7.2.3 Biomechanics of chewing	112
7.2.4 Fusion of the mandibular symphysis	113
7.3 Zone of variability	114
CHAPTER 8: Conclusion	116
8.1 Overview	116
8.2 Summary of results	116
8.3 Re-evaluating Schultz's Rule	117
8.4 Future directions	117
8.4.1 Sample size	117
8.4.2 Better resolution of the fossil record	118
8.4.3 The anterior dentition	118
8.4.4 Sampling in other taxa	118
8.5 Importance of this study	119

REFERENCES
APPENDICES

120
141

List of Tables

Table 1. Primate and primate-outgroup sample examined by TM, categorized by family	9
Table 2. Primate and primate-outgroup sample examined by TM, categorized by genus	10
Table 3. Primate and primate-outgroup sample examined by TM, categorized by species	
a. Catarrhines, 1 of 2	11
b. Catarrhines, 2 of 2	12
c. Platyrrhines	13
d. Strepsirrhines, Dermopterans	14
Table 4. Primate and primate-outgroup sample from the literature, by major clade	15
Table 5. Primate and primate-outgroup sample from the literature, by family	16
Table 6. References for the primate dental eruption sequences from the literature	17
Table 7. Artiodactyls examined by TM, by family	19
Table 8. Artiodactyls examined by TM, by genus	
a. Antilocapridae, Bovidae	20
b. Bovidae, Camelidae, Cervidae, Giraffidae	21
c. Hippopotamidae, Moschidae, Suidae, Tayassuidae, Tragulidae	22
Table 9. Primate and primate-outgroup dental eruption sequences as assessed by TM	
a. Catarrhines	35
b. Catarrhines (cont.), Platyrrhines, Strepsirrhines, Dermopterans	36
Table 10. Primate and primate-outgroup dental eruption sequences	
a. Catarrhines	37
b. Catarrhines (cont.), Platyrrhines	38
c. Platyrrhines (cont.), Strepsirrhines	39
d. Strepsirrhines (cont.), Tarsiiformes, Adapiformes, Plesiadapiformes, Dermopterans, Scandentia	40
Table 11. Sample size (genus) of determined dental eruption sequences in primates	41
Table 12. Sample size (species) of determined dental eruption sequences in primates	
a. Catarrhines, Platyrrhines	42

b. Strepsirrhines, Tarsiiformes, Adapiformes, Plesiadapiformes, Dermoptera, Scandentia	43
Table 13. Primate sample collected by TM, breakdown by sex	
a. Catarrhines	44
b. Catarrhines (cont.), Platyrrhines, Strepsirrhines, Dermopterans	45
Table 14. Specimen numbers of the primates and primate-outgroups used to assess dental eruption sequence	
a. Catarrhines	46
b. Catarrhines (cont.)	47
c. Platyrrhines	48
d. Platyrrhines (cont.), Strepsirrhines	49
e. Strepsirrhines (cont.), Tarsiiformes, Adapiformes, Plesiadapiformes, Dermoptera, Scandentia	50
Table 15. Test of intraspecific variation in <i>Cebus</i>	51
Table 16. Intraspecific variation in dental eruption sequence in <i>Alouatta</i>	53
Table 17. Intraspecific variation in dental eruption sequence in <i>Saimiri</i>	54
Table 18. Intra- and interspecific variation in dental eruption sequence in <i>Presbytis</i>	54
Table 19. Results of TM's examination of artiodactyl dental eruption sequence	59
Table 20. Artiodactyl dental eruption sequences as assessed by TM	62
Table 21. Total sample size of determined dental eruption sequences in artiodactyls	65
Table 22. Artiodactyl sample collected by TM, breakdown by sex	66
Table 23. Specimen numbers of the artiodactyls used to assess dental eruption sequence	69
Table 24. Descriptive statistics for life history and body size variables for primate species in which the premolars erupt last	76
Table 25. Descriptive statistics for life history and body size variables for primate species in which the molars erupt last	76
Table 26. Descriptive statistics for life history and body size variables for artiodactyl species in which the fourth premolar erupts last	77
Table 27. Descriptive statistics for life history and body size variables for artiodactyl species in which the third molar erupts last	77

Table 28. Phylogenetic independent contrasts between dental eruption sequence and life history/body size traits in primates	82
Table 29. Phylogenetic independent contrasts between dental eruption sequence and life history/body size traits in artiodactyls	82
Table 30. Tests of phylogenetic signal in primates	84
Table 31. Tests of phylogenetic signal in artiodactyls	84
Table 32. Likelihood (%) of each dental eruption sequence at each ancestral state node on the primate phylogeny	91
Table 33. Likelihood (%) of each dental eruption sequence at each ancestral state node on the artiodactyl phylogeny	96
Table 34. Fossils examined by TM for this study	105

List of Figures

Figure 1.	Examples of eruption sequence in primates	26
Figure 2.	Examples of eruption sequence in artiodactyls	27
Figure 3.	Examples of variation in dental eruption sequence in <i>Alouatta</i>	34
Figure 4.	The distribution of dental eruption sequences across subfamily Caprinae	58
Figure 5.	Phylogeny of all primate species for which dental eruption sequence is reported in this study	78
Figure 6.	Phylogeny of all artiodactyl species for which dental eruption sequence is reported in this study	79
Figure 7.	Results of the maximum likelihood ancestral state reconstruction in primates	89
Figure 8.	Results of the parsimony ancestral state reconstruction in primates	90
Figure 9.	Results of the maximum likelihood ancestral state reconstruction in artiodactyls	94
Figure 10.	Results of the parsimony likelihood ancestral state reconstruction in artiodactyls	95
Figure 11.	Example of a catarrhine dental eruption sequence in a fossil maxilla, cercopithecoid specimen UCMP 56610 (palatal view)	102
Figure 12.	Example of a catarrhine dental eruption sequence in a fossil mandible, cercopithecoid specimen UCMP 56660 (occlusal view)	103
Figure 13.	Example of a catarrhine dental eruption sequence in a fossil mandible, cercopithecoid specimen UCMP 125858	104

List of Appendices

Appendix A. Test of intraspecific variation in <i>Ovis</i> , mandibular raw data	141
Appendix B. Test of intraspecific variation in <i>Ovis</i> , maxillary raw data	149
Appendix C. Life history and body size variables for the primate sample, raw data	157
Appendix D. Life history and body size variables for the artiodactyl sample, raw data	163

Acknowledgements

I would like to start by first acknowledging my dissertation committee, Leslea Hlusko, Charles Marshall and Jun Sunseri, without whom this dissertation would not have been possible. They spent many hours offering comments and critiques that greatly improved this dissertation, and I am very grateful to have been able to pick their brains on all matters biology, anthropology, and academia. I would like to especially thank Leslea Hlusko for advising me through the craziness that we call a PhD program. She is a strong, confident, and well-reasoned scientist, and I am proud to call her a mentor, particularly in a time when it is not as easy to find a female role model in science as it probably should be. I am happy to have come into my own as a scientist under her guidance. I would also like to thank my qualifying exam committee for the many hours they spent with me leading up to, and during the exam: Charles Marshall, Tom Carlson, Bill Clemens, and Craig Miller.

My lab has been a welcoming and inspiring place to spend the last five years, and I would like to acknowledge labmates Marianne Brasil and Whitney Reiner, as well as past labmate Theresa Grieco. In today's scientific atmosphere, it is a comfort and pure delight to spend my time in an intellectual environment fueled by such amazing scientists. Being able to bounce my ideas off of them, being able to get advice on navigating the department, and being able to de-stress by talking about life in the Bay not only helped me make it through graduate school but made me a better person and better scientist during the process. These are things I will take with me for life. Marianne in particular, with whom I have spent so much research time over the last five years, has had a profound impact on my life. Marianne, you are a remarkable scientist and an even more remarkable person.

I would also like to acknowledge the Human Evolution Research Center community, and especially Tim White, Josh Carlson, and Antoine Souron for their discussion and feedback, and of course, for their delightful storytelling. Marvalee Wake, David Ackerly, Chris Emerling, Philip Skipwith, Tanya Smith, and Andrew Weitz also donated their time to help me learn new methods and analyses, and provided extremely helpful dialogue on the problems of my dissertation.

Funding for this dissertation research and presentation of results was provided by the UC Chancellor's Fellowship from UC Berkeley, the Jerry O. Wolff Fellowship from the Museum of Vertebrate Zoology, the Lakhon-Pal Fellowship and The Robert and Nancy Beim Endowed Graduate Field Research Fund from the Department of Integrative Biology at UC Berkeley, graduate student funding from the UC Museum of Paleontology, and the Desmond Clark Graduate Fellowship from the Human Evolution Research Center.

I would also like to thank my family for their support, and particularly my fiancé Andrew Weitz. I can say with absolute certainty that this dissertation would not have been possible without the support, encouragement, comfort, and love that Andrew gave to me during this long and arduous process. Additionally, many of my intellectual advancements have been the product of early morning biology talks over coffee, or late night drive home musings about ecology and evolution. Andrew, you are a truly exceptional person, and you make me a better scientist. I look forward to many, many more years of conversations with you about science, evolution, ecology, and of course, teeth.

CHAPTER 1: Mammalian dental eruption sequence

1.1 Overview

This dissertation investigates the relationship between dental eruption sequence, life history, and phylogeny in mammals. As an introduction, this chapter gives background on the evolution of mammalian dentition and recounts the history of study of dental eruption sequence, including Schultz's seminal work (1935) and Smith's (2000) more recent naming of Schultz's Rule. Alternate hypotheses about the relationship between dental eruption sequence and phylogeny are also reviewed. The two hypotheses to be tested in this dissertation are presented, and the chapter concludes with a summary outline of the dissertation and details about all of the subsequent chapters. A summary of the materials used in this dissertation are described in the next chapter (Chapter 2).

1.2 Evolution of the dentition

The dentition is one of the most important organs of the mammalian body, as teeth play a significant role in fitness and reproduction (e.g., Bryant 1990, McCollum and Sharp 2001, Swindler 2002, Hillson 2005, Leigh et al. 2008, Ungar 2010). Teeth only evolved in vertebrates a single time, and they are hypothesized to have emerged via one of two likely scenarios: 1) teeth are derived from the internalization of skin denticles either after, or simultaneously with, the evolution of jaws (e.g., Reif 1982, Smith and Hall 1993, Smith and Coates 2001), or teeth are derived from internal pharyngeal denticles, independently of the jaws (e.g., McCollum and Sharpe 2001, Smith and Coates 2001). Fossil evidence increasingly supports the latter - evolution of teeth before jaws (e.g., Smith and Coates 2001). Dental variation has given rise to a range of diverse morphologies (particularly within mammals), while still maintaining a high-level of similarity in type, number, and developmental origins (e.g., McCollum and Sharp 2001, Swindler 2002, Hillson 2005).

1.3 Dental eruption sequence

Most mammals are diphyodont, meaning they have two generations of teeth: the deciduous (milk) teeth and the adult teeth. These two generations allow for size and complexity of the teeth 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 timing of permanent tooth development, the size of the face and dental arch, life history, juvenile and adult diets, and even group dynamics as represented by intrasex competition (e.g., Schultz 1935, 1956, Bryant 1990, Smith 1994, 2000, Leigh et al. 2008).

Tooth eruption has been well-studied in mammals, and a great deal is known about the biology of tooth eruption including the processes of resorption and the cellular and molecular processes associated with eruption (e.g., Cahill 1969, Marks 1973, Cahill et al. 1988, Wise et al. 2002). However, less is known about the factors driving the timing and sequence of dental

eruption (e.g., Woodroffe et al. 2010, Kjær 2014). 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 in diet and competition/defense, and is likely 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 has also been considerable interest in the dental eruption sequence of fossil mammals, including primates (e.g., Gregory 1920, Lamberton 1938, Wallace 1977, Kay and Simons 1983), whales (Kellogg 1936), and other extinct groups (e.g., Ciffeli and de Muizon 1998, Lucas and Schoch 1990).

Because of this paleontological interest, and in order to understand the implications of fossil dental eruption sequences, it has become imperative to understand the factors influencing dental eruption sequence in extant mammals. Over the last century, two major hypotheses about dental eruption sequence in mammals have arisen: 1) Dental eruption sequence is adaptive and associated with life history variables like post-natal growth and longevity (Schultz 1956, 1960, Smith 1994, 2000), or 2) 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).

1.3.1 Schultz's study of dental eruption sequence

One of the first and most influential studies on dental eruption sequence was published by Adolph Schultz in 1935. Schultz's interest in dental eruption sequence originated in methods of age estimation in primates which continue to rely on stages of dental eruption wear. Schultz (1935) assessed dental eruption stages in 12 living primates (macaques and chimps) as well as in a large sample of dead specimens, focusing exclusively on haplorhines. Overall, Schultz (1935) was able to examine $n=2,908$ primate specimens from his own collection and at five U.S. museums. In this study, Schultz (1935) reports the age at eruption for macaques, chimps, and humans, as well as dental eruption sequences for four New World monkeys (*Cebus*, *Saimiri*, *Ateles*, and *Alouatta*), four apes (*Gorilla*, *Pongo*, *Pan*, and *Hylobates*), and five Old World monkeys (*Pithecia*, *Papio*, *Lasiopgya* [now *Cercopithecus*], *Colobus*, and *Pygathrix*). Schultz (1935) notes some intrageneric variation in dental eruption sequence, particularly in *Alouatta* and *Saimiri*. He concludes that all primates in his study erupt the M3 last, with the exception of *Pygathrix* and *Saimiri* (mandible only, Schultz 1935). In this paper, Schultz (1935) states that dental eruption sequence has a phylogenetic signal that can be used to reconstruct phylogenetic relationships in primates, particularly primitive versus derived species.

In two influential manuscripts on post-embryonic age changes in primates, Schultz (1956, 1960) expanded on this earlier work on dental eruption sequence. He noted that many species of primate have delayed eruption of the third molar, with humans as the most extreme example of this delay, presenting a table of dental eruption sequences in 11 genera of primates as well as a generalized category that distinguish the "majority of monkeys and all apes" (Schultz 1956:12). After considering the dental eruption sequences of his primate sample, Schultz wrote that, "There can be little doubt that these ontogenetic specializations represent necessary adaptations to the gradual prolongation of the period of post-natal growth" (Schultz 1956:13). He further expanded on his hypothesis by theorizing that, "only in the rapidly maturing, primitive forms can the entire dental row be completed before the delicate milk teeth need to be replaced" (Schultz 1960:938). Since Schultz (1935, 1956, 1960) proposed that dental eruption sequence is an adaptation to rates of post-natal growth, his work has been cited hundreds of times.

Building off of work investigating the relationship between brain size and life history variables (e.g., Sacher, 1959, 1975, 1978, Sacher and Staffeldt 1974), Smith (1989) collected data on age at M₁ eruption (mandible), and age at completed dental eruption, for 21 species of primate spanning seven families. Smith (1989) found that age at M₁ eruption is highly correlated with brain size ($r=0.98$). Although also correlated, Smith (1989) reports that the correlations between brain size and other life history traits (e.g., gestation length, female sexual maturity, and lifespan) are much lower ($r=0.48-0.68$). Smith (1989) also cites Harvey and Clutton-Brock (1985) in noting the positive correlation between body size and some life history traits, and she postulates that high correlations between dental eruption ages and brain size likely also indicate that the study of dental eruption sequence is important in understanding the evolution of life history.

In order to expand on her earlier work, and to further test hypotheses about the relationship between dental eruption sequence and life history, Smith (1994) compiled a comprehensive list of primate dental eruption sequences from the literature and added in data for four new species, finding that age at dental eruption is strongly correlated with both body and brain size. The age of tooth eruption is also correlated across teeth (Smith 1994). For example, Smith (1994) reports that the age at eruption of the deciduous premolars is highly correlated with the age at eruption of the permanent premolars ($r=0.95-0.96$, Smith 1994:194).

From this interest in dental eruption ages, Smith (2000) turned to an investigation of dental eruption sequence. Based on all of Schultz's work (1935, 1956, 1960), and following her own analyses, Smith (2000) proposed Schultz's Rule, which states that replacement teeth erupt earlier relative to the molars in long-lived species with a slower rate of growth, also known as a slower life history. Smith (2000) tested Schultz's Rule in primates and ungulates, comparing dental eruption sequence and a measure of growth speed, classified by proxy of age at emergence of the first molar. Smith (2000) reports that faster-growing species erupt the molars earlier in the sequence while slower growing species erupt the molars later in the sequence. Smith (2000) also found that maximum lifespan is significantly correlated with dental eruption sequence in both primates and ungulates (calculated by the eruption of either I₁ or P₃ relative to the mandibular molars). Within her sample, Smith (2000) finds that body size and brain weight are also correlated with dental eruption sequence in primates, but not in ungulates. Overall, Smith (2000) suggests that ungulates tend to follow Schultz's Rule, and primates appear to adhere to it tightly.

Smith's (2000) work on Schultz's Rule has been cited extensively in the interpretation of life history and dental eruption sequence in extant and, particularly, fossil primates (e.g., Schwartz et al. 2005, Robson and Wood 2008, Franzen et al. 2009), as well as other mammals (e.g., Macho and Williamson 2002, Loe et al. 2004, Asher and Olbricht 2009, Dirks et al. 2009, McGee and Turnbull 2010, Townsend and Croft 2010, Yamanaka et al. 2010, Billet and Martin 2011), and even marsupials (Van Nievelt and Smith 2005). Researchers have also published support for Schultz's Rule in the form of correlations between individual taxa, dental eruption sequence, and the pacing of life history and post-natal growth (e.g., Hellmund 2013, 2016, Jordana et al. 2013).

1.3.2 Hypotheses on the relationship between dental eruption sequence and phylogeny

As a counterpoint to Schultz's hypothesis that dental eruption sequence is related to life history and rates of post-natal growth, several researchers have argued that dental eruption sequence, whether or not it is correlated with other factors, has a conserved phylogenetic signal

(Schwartz 1974, Tattersall and Schwartz 1974, Byrd 1981, Veitschegger and Sánchez-Villagra 2016). Additionally, Schultz's Rule has been challenged by authors studying groups of primates (Godfrey et al. 2005, Guthrie and Frost 2011, Jogahara and Natori 2012), and other mammals (Veitschegger and Sánchez-Villagra 2016).

In his dissertation, Schwartz (1974) extensively examined dental eruption sequence in prosimians and found that almost all prosimians erupt the M3 before one or more of the premolars. He assumes a phylogenetic signal to this homogeneity, reconstructing a likely ancestral dental eruption sequence where the M1 erupts first, and where the M3 erupts before several of the premolars (Schwartz 1974, Tattersall and Schwartz 1974). From a large sample, Schwartz (1974) also notes that the sequence of initial eruption (when the crown starts to show) is not always the same as the final eruption sequence (when the crown is in occlusion), meaning that teeth may begin erupting in one sequence, and then, due to variation in eruption speed, complete erupting in a different sequence. Byrd (1979, 1981) also used Schultz's (1935) work, in conjunction with studies by Schwartz (1974) and Tattersall and Schwartz (1974), to advance phylogenetic hypotheses about New World monkey family, Callitrichidae.

Smith (2000) noted that lemurs, in particular, do not seem to follow Schultz's Rule, an observation that has been extrapolated on by Godfrey et al. (2005). In their work, Godfrey et al. (2005) assess dental eruption sequence in *Avahi* and *Lepilemur*, supplementing Smith's (2000) data. With these new data, they refute Smith's (2000) hypothesis that a toothcomb is responsible for the dental eruption sequence seen in lemurs, and they also challenge Schultz's Rule and its power to explain dental eruption sequence through rates of post-natal growth (Godfrey et al. 2005).

Most recently, Veitschegger and Sánchez-Villagra (2016) attempted to more fully test Smith's (2000) hypothesis that Schultz's Rule can be applied to cervids in the same manner as primates. They collected dental eruption sequences for 25 extant and extinct cervids, examining mandibles of specimens from seven museums as well as collecting data from the literature. Veitschegger and Sánchez-Villagra (2016) report variation in dental eruption sequence, and they conclude that Schultz's Rule does not apply to cervids. According to their analyses, dental eruption sequence in cervids is not associated with lifespan, age at sexual maturity, brain or body mass, or age at weaning (Veitschegger and Sánchez-Villagra 2016). Instead, in cervids, dental eruption sequence is directly influenced by phylogeny (Veitschegger and Sánchez-Villagra 2016).

1.4 Research questions and hypotheses

This history of research demonstrates significant disagreement on whether life history variables or phylogeny, or possibly other factors, are driving the evolution of dental eruption sequence. In large part because of Schultz's (1935) work, primates have been a primary focus of many studies on dental eruption sequence, but Schultz's Rule (Smith 2000) has been applied to many studies of extant and fossil mammals (e.g., Macho and Williamson 2002, Loe et al. 2004, Schwartz et al. 2005, Robson and Wood 2008, Asher and Olbricht 2009, Dirks et al. 2009, Franzen et al. 2009, McGee and Turnbull 2010, Townsend and Croft 2010, Yamanaka et al. 2010, Billet and Martin 2011). Because of this focus on primates and artiodactyls in past studies, and the seemingly contradictory results among them, I chose to focus on these two groups in an attempt to resolve the puzzle.

In this study, I add to the primate and artiodactyl dental eruption sequence literature by examination of more than 8,000 specimens spanning more than 200 species at the Museum of Vertebrate Zoology in Berkeley, California, and the Smithsonian National Museum of Natural History in Washington, D.C. Using these specimens, along with data gleaned from the literature, I aim to address two main hypotheses:

Hypothesis 1:

H1₀) Dental eruption sequence is not correlated with life history or body size.

H1_A) Dental eruption sequence is significantly correlated with life history and body size variables that capture post-natal growth and longevity (Schultz's Rule).

Hypothesis 2:

H2₀) Dental eruption sequence does not have a phylogenetic signal in either primates or artiodactyls

H2_A) Dental eruption sequence is phylogenetically conserved, or more similar in more closely related genera. It is also possible that dental eruption sequence is phylogenetically conserved in one group and not the other (conserved in primates but not artiodactyls, or vice-versa).

1.5 Dissertation overview

In order to test these hypotheses, I conducted a comprehensive examination of dental eruption sequence in Primates and Artiodactyla. A complete breakdown of the sample used in this study, of both primates and artiodactyls, is presented in Chapter 2. The methods used to assess dental eruption sequence are discussed in Chapter 3, followed by a detailed summary of dental eruption sequences for all of the primates and artiodactyls examined in this study, and supplemented by data from the literature. All of the analytical methods used in this study are given their own chapters (Chapters 3, 4, 5, and 6). In each of these analytical chapters, a description of the analysis and the methods are detailed, followed by a presentation of the results of the analysis, first for the primates and then for the artiodactyls. I test both hypotheses in Chapter 4 with tests for phylogenetic signal and phylogenetic independent contrasts of dental eruption sequence and life history and body size traits. The ancestral state reconstruction is presented in Chapter 5, and I detail the hypotheses about the likelihood of dental eruption sequences at particular ancestral nodes. Fossil dental eruption sequences, collected both by examination and from the literature, are presented and compared to the results of the ancestral state reconstruction in Chapter 6. In the discussion (Chapter 7), I present several hypotheses on factors that may be driving the evolution of dental eruption sequence in primates and artiodactyls. The discussion is followed by a conclusion and comprehensive summary of the results of this study (Chapter 8). The results for artiodactyls were previously published as an independent body of work in the *Journal of Mammalian Evolution* (Monson and Hlusko 2016).

CHAPTER 2: Materials used in the assessment of dental eruption sequence

2.1 Overview

Built largely from Schultz's work (1935, 1956, 1960), and expanded by Smith (2000), the large majority of research on dental eruption sequence has focused on either primates or artiodactyls. Because of this, I chose to focus on the same taxa to test my hypotheses, reviewing their basic biology and ecology in this chapter. What is known about primate evolution from fossils and molecular data is presented first, followed by the artiodactyls. I also present a complete breakdown of the primate and artiodactyl samples used in the study, by family, genus, species, and by specimens examined. For the primates, I collected supplementary data on dental eruption sequence from the literature, and I compare the breakdown of specimens collected by TM and from the literature below. Following the discussion of the materials in this chapter, a full description of the the distribution of dental eruption sequences across extant taxa is presented in Chapter 3. Both hypotheses about dental eruption sequence are tested in Chapter 4, followed by an ancestral state reconstruction of dental eruption sequence (Chapter 5) with incorporation of fossil specimens (Chapter 6).

2.2 Evolution of the primates

Primates are a diverse order composed of more than 400 species across Africa, Asia, and South America (Nowak 1999, Rylands and Mittermeier 2014), a number that continues to grow with the discovery of new species (e.g., Jones et al. 2005, Merker and Groves 2006). Based on the fossil record, extinct primates also flourished in North America and Europe (Szalay and Delson 1979, Hartwig 2002). Molecular data points to the origin of primates in the late Cretaceous, approximately 60-80 MA (Steiper and Young 2006, Soligo et al. 2007, Rosenberger and Hartwig 2013), and the earliest fossils definitively date the origin of the group to the Eocene, approximately 55 MA (Covert 2002, Soligo et al. 2007).

Primates are varied in size, morphology, diet, behavior, etc. Body size ranges from the smallest primate, *Microcebus*, the mouse lemur, averaging 30 grams, to *Gorilla*, an extant ape that can weigh more than 200 kilograms (Mittermeier et al. 1999, Nowak 1999). Many primates have evolved a primarily arboreal locomotor system, and the resulting morphological adaptations associated with this lifestyle have influenced the evolution of vision, brain size, morphology of the hands and feet, and countless other attributes of physiology and behavior (Mittermeier et al. 1999, Nowak 1999). Within the primates, there are also several important dietary and non-dietary dental adaptations, including the continuously growing incisors of the aye-aye and the incisor toothcomb of the lemuriformes (Hillson 2005). The primate diet ranges from all parts of plant material (barks, fruits, leaves, shoots, flowers, nectar, and even gum), to fungi, to vertebrates and invertebrates (Mittermeier et al. 1999, Nowak 1999).

2.2.1 The earliest primates

The earliest primates are Omomyoidea and Adapoidea, extinct taxa of which fossils have been recovered in Africa, Asia, the Middle East, Europe, and North America, primarily dated to the Eocene (Covert 2002), although fossil discoveries indicate their persistence into the

Oligocene and Miocene (Beard 1998, Köhler and Moyà-Solà 1999, Chaimanee 2010). Debates continue on the relationship between omomyoids and adapoids and extant primates (e.g., Fleagle and Kay 1994, Dagosto et al. 1996, Covert 2002). One hypothesis is that omomyoids gave rise to the eosimiids and tarsiids, and the adapoids gave rise to the lorisooids and lemuroids (Covert 2002). Phylogenetic analyses place adapoids as sister taxa to extant strepsirrhines (e.g., Seiffert et al. 2009, Williams et al. 2010), although there is no consensus on which adapoid group may have given rise to extant taxa (Covert 2002), and there is little to no evidence for a direct phyletic relationship (Seiffert et al. 2005, Godinot 2006, Fleagle 2013). The last common ancestor of strepsirrhines and anthropoids marks the divergence of crown primates and has been dated at approximately 77.5 MA (Steiper and Young 2006), essentially at the last common ancestor for euprimates (Covert 2002, Steiper and Young 2006, Soligo et al. 2007, Rosenberger and Hartwig 2013).

2.2.2 Evolution of the tarsiiformes

The phylogenetic placement of the tarsiers, as either monophyletic with the anthropoids or the strepsirrhines, has been a source of debate for the last 40 years (e.g. Simons 1976, Gingerich 1981). Fossil evidence indicates that tarsiiformes existed as early as the earliest Eocene (Gunnell and Rose 2002), but *Tarsius* is the only extant tarsiiform, and the only tarsiiform to persist past the end of the Eocene (Gunnell and Rose 2002). This early divergence date has made the relationship between tarsiers and anthropoids, relative to the strepsirrhines, difficult to describe with certainty (Gunnell and Rose 2002). Some researchers use the primitive dentitions of tarsiers to group them with lemurs and lorises as Prosimii, to the exclusion of Anthropoidea (e.g., Gingerich 1981, Simons and Rasmussen 1989), a position which has received some support from DNA analyses (e.g., Murphy et al. 2001, Schmitz et al. 2002). Other researchers use evidence from soft anatomical features of extant primates, characters that are rarely preserved in the fossil record, to group tarsiers with anthropoids as Haplorhini, to the exclusion of lemurs and lorises, the Strepsirrhini (e.g., Szalay and Delson 1979, Kay et al. 1997, Gunnell and Rose 2002). Like the Prosimii/Athropoidea classification, the Haplorhini/Strepsirrhini classification has received support from molecular analyses (e.g., Schmitz et al 2001, Jameson et al. 2011). Based on the molecular data used in this study (see Chapter 4 for methods on building phylogenies), the tarsiers are placed in a monophyletic clade with the anthropoids as the haplorhines, independent of the strepsirrhines. When the strepsirrhines and tarsiers are grouped as a paraphyletic clade to compare them with the anthropoids, they are termed prosimians (e.g., Beard 2002).

2.2.3 Evolution of the anthropoids

Living anthropoids are classified into two groups: Catarrhini, the Old World monkeys and apes, including humans, and Platyrrhini, the New World monkeys (e.g., Dagosto 2002). Based on fossil evidence in South America, the divergence of the catarrhines and platyrrhines occurred at least as early as the Oligocene (e.g., Dagosto 2002). Additional fossil evidence from the Eocene of China has been used to argue that the anthropoids originated early in the Cenozoic (Beard and MacPhee 1994, Beard et al. 1994), although some researchers are not convinced (Godinot 1994, Simons and Rasmussen 1994). Overall, basal anthropoids are fairly well-represented by fossils from the middle Eocene and Oligocene, spanning northern Africa to

China, many of which preserve important anatomy critical to understanding the evolution of this clade (Beard 2002). Additionally, molecular data support an early divergence of the anthropoids based on robust support for the clade, as well as monophyly, both lines of evidence for a long period of common descent (Beard 2002). While debates about the ancestral stock from which anthropoids are derived continue, fossil evidence points to an Asian origin for the clade (Beard 2002). Additionally, it is now widely agreed that anthropoids and prosimians diverged over millions of years, with the diagnostic traits separating them evolving gradually over time (Beard 2002).

2.2.4 Evolution of the strepsirrhines

The strepsirrhines, made up of lemuriformes and lorises, have a fossil record that stretches back to the Eocene (Phillips and Walker 2000). The divergence of these two subgroups has been estimated at approximately 50-80 MA (e.g., Roos et al. 2004), and the fossil record suggests that Lorisidae and Galagidae both evolved in Africa (Phillips and Walker 2000, Seiffert et al. 2003). Endemic to the island of Madagascar, lemurs are estimated to have arrived there sometime in the Eocene (Godfrey and Jungers 2002). This estimation is based on molecular data, as the stratigraphically shallow fossil record of Madagascar island only extends to ~ 26,000 years BP in many areas of the island (Godfrey and Jungers 2002). In no small part because of this limited fossil record, the nature of the divergence, and subsequent phylogenetic relationships among lemurs remain controversial (e.g., Tattersall and Schwartz 1974, Kolnicki 1999, Delpore et al. 2001, Roos et al. 2004).

2.3 Description of the primate sample

In order to thoroughly sample dental eruption sequence in primates beyond what has been described in the literature, I assessed postcanine dental eruption sequence in a sample of n=4,134 extant primates and primate outgroups, spanning 10 families. All specimens are held in the Smithsonian National Museum of Natural History in Washington, D.C. The sample includes data from 31 genera and 105 species of primate and primate-outgroup, all examined by TM. I present a breakdown of the sample examined by family (Table 1), genus (Table 2) and species (Table 3). Many of the primate genera, such as *Cebus*, *Hylobates*, *Trachypithecus*, and *Eulemur*, had more than five species represented. Catarrhines are the largest and most diverse clade of primates (e.g., Nowak 1999), and they have the greatest genus and species representation in this study. Overall, the majority of the primate specimens I examined for this study are catarrhines.

Because so much work has already been done to compile dental eruption sequences, I focused on species and genera that are less well-represented in the literature, and I relied on published data for species such as *Homo sapiens*, *Papio hamadryas*, and *Macaca mulatta*. I also focused on primates that have all three molars and therefore excluded New World monkey genera that lack the third molars (e.g., *Leontopithecus*). With the exception of *Saimiri*, I examined every specimen available for the species listed in Tables 1 to 3.

In addition to the 33 genera and 105 species I examined, I collected data on dental eruption sequence for 32 genera from the literature. Most of the genera collected from the literature are catarrhines or strepsirrhines. Two outgroup taxa, both Scandentia, are represented exclusively by data collected from the literature. Additionally, I collected data on six fossil species from the literature: extinct lemurs *Archaeolemur* (two species) and *Hadropithecus*, fossil

strepsirrhine *Megaladapis*, adapiforme *Adapis*, and plesiadapid *Acidomomys*. All extinct taxa are marked by a cross (†). With the exception of *Archaeolemur* and *Lemur*, the dental eruption sequence for only one species for each genus was taken from the literature. I present the breakdown of genera collected by TM and from the literature by major clade (Table 4), and family (Table 5). A list of references for the dental eruption sequences from the literature is available in Table 6.

Table 1 Primate and primate-outgroup sample examined by TM, categorized by family

Clade	Family	Genus	Species (n)	Specimens examined (n)
Catarrhine	Cercopithecidae	13	45	988
	Hylobatidae	3	10	185
	Total	16	55	1,173
Platyrrhine	Atelidae	3	17	1,491
	Callitrichidae	1	1	12
	Cebidae	2	7	1,165
	Pitheciidae	2	4	92
	Total	8	29	2,760
Strepsirrhine	Daubentoniidae	1	1	2
	Indriidae	1	7	17
	Lemuridae	4	11	74
	Lorisidae	1	2	5
	Total	7	21	98
Dermoptera	Cynocephalidae	2	2	103
	Total	2	2	103
GRAND TOTAL		33	105	4,134

Table 2 Primate and primate-outgroup sample examined by TM, categorized by genus

Clade	Family	Genus	Species (n)	Specimens examined (n)	
Catarrhine	Cercopithecidae	<i>Allenopithecus</i>	1	4	
		<i>Cercocebus</i>	3	52	
		<i>Chlorocebus</i>	1	49	
		<i>Colobus</i>	5	132	
		<i>Erythrocebus</i>	1	34	
		<i>Lophocebus</i>	1	25	
		<i>Miopithecus</i>	1	59	
		<i>Presbytis</i>	11	237	
		<i>Ptilocolobus</i>	4	49	
		<i>Pygathrix</i>	2	22	
		<i>Rhinopithecus</i>	1	13	
		<i>Semnopithecus</i>	5	34	
		<i>Trachypithecus</i>	9	278	
		Hylobatidae	<i>Hylobates</i>	6	151
			<i>Nomascus</i>	3	15
<i>Symphalangus</i>	1		19		
Total			55	1,173	
Platyrrhine	Atelidae	<i>Alouatta</i>	6	1,085	
		<i>Ateles</i>	8	360	
		<i>Lagothrix</i>	3	46	
	Callitrichidae	<i>Callimico</i>	1	12	
	Cebidae	<i>Cebus</i>	6	933	
		<i>Saimiri</i>	1	232	
	Pitheciidae	<i>Chiropotes</i>	2	56	
		<i>Pithecia</i>	2	36	
	Total			29	2,760
Strepsirrhine	Daubentoniidae	<i>Daubentonia</i>	1	2	
	Indriidae	<i>Propithecus</i>	7	17	
		<i>Eulemur</i>	7	38	
	Lemuridae	<i>Haplemur</i>	1	10	
		<i>Lemur</i>	1	13	
		<i>Varecia</i>	2	13	
	Lorisidae	<i>Arctocebus</i>	2	5	
Total			21	98	
Dermoptera	Cynocephalidae	<i>Cynocephalus</i>	1	20	
		<i>Galeopterus</i>	1	83	
		Total	2	103	
GRAND TOTAL			105	4,134	

Table 3a Primate and primate-outgroup sample examined by TM, categorized by species (Catarrhines)*

Clade	Family	Genus	Species	Specimens examined (n)	
Catarrhine	Cercopithecidae	<i>Allenopithecus</i>	<i>nigroviridis</i>	4	
			<i>Cercocebus</i>	<i>agilis</i>	2
		<i>atys</i>		22	
		<i>torquatus</i>		27	
		sp.		1	
		<i>Chlorocebus</i>		<i>aethiops</i>	49
				<i>Colobus</i>	<i>angolensis</i>
		<i>guereza</i>			99
		<i>polykomos</i>			11
		<i>satanas</i>			6
		<i>vellerosus</i>			3
		sp.			2
		<i>Erythrocebus</i>	<i>patas</i>		34
		<i>Lophocebus</i>	<i>albigena</i>		25
		<i>Miopithecus</i>	<i>ogouensis</i>	59	
		<i>Presbytis</i>	<i>chrysomelas</i>	16	
			<i>comata</i>	3	
			<i>femoralis</i>	19	
			<i>frontata</i>	29	
			<i>hosei</i>	35	
			<i>melalophos</i>	30	
			<i>natunae</i>	8	
			<i>potenziani</i>	19	
		<i>rubicunda</i>	49		
		<i>siamensis</i>	18		
		<i>thomasi</i>	11		
			Total	592	

Table 3b Primate and primate-outgroup sample examined by TM, categorized by species (Catarrhines (cont.))*

Clade	Family	Genus	Species	Specimens examined (n)	
Catarrhine	Cercopithecidae	<i>Ptilocolobus</i>	<i>badius</i>	43	
			<i>foai</i>	2	
			<i>kirkii</i>	3	
			<i>tephrosceles</i>	1	
		<i>Pygathrix</i>	<i>nemaeus</i>	12	
			<i>nigripes</i>	10	
			<i>roxellana</i>	13	
		<i>Rhinopithecus</i>	<i>entellus</i>	6	
		<i>Semnopithecus</i>	<i>johnii</i>	2	
			<i>priam</i>	4	
			<i>schistaceus</i>	6	
			<i>vetulus</i>	15	
			sp.	1	
			<i>Trachypithecus</i>	<i>auratus</i>	22
				<i>cristatus</i>	163
				<i>ebenus</i>	1
				<i>germaini</i>	11
				<i>obscurus</i>	32
		<i>phayrei</i>		46	
		<i>pileatus</i>		1	
		<i>poliocephalus</i>		1	
	<i>shortridgei</i>	1			
	Hylobatidae	<i>Hylobates</i>		<i>agilis</i>	22
			<i>hoolock</i>	4	
			<i>klossii</i>	16	
			<i>lar</i>	53	
			<i>muelleri</i>	40	
			<i>pileatus</i>	12	
			sp.	4	
			<i>Nomascus</i>	<i>concolor</i>	5
				<i>gabriellae</i>	2
<i>leucogenys</i>				8	
<i>Symphalangus</i>	<i>syndactylus</i>	19			
			Total	581	

Table 3c Primate and primate-outgroup sample examined by TM, categorized by species (Platyrrhines)*

Clade	Family	Genus	Species	Specimens examined (n)
Platyrrhine	Atelidae	<i>Alouatta</i>	<i>belzebul</i>	27
			<i>caraya</i>	34
			<i>coibensis</i>	303
			<i>palliata</i>	417
			<i>pigra</i>	153
			<i>seniculus</i>	151
		<i>Ateles</i>	<i>ater</i> (sp.)	18
			<i>belzebuth</i>	34
			<i>chamek</i>	10
			<i>fusciceps</i>	58
			<i>geoffroyi</i>	169
			<i>hybridus</i>	59
			<i>marginatus</i>	4
			<i>paniscus</i>	8
	<i>Lagothrix</i>	<i>lagotricha</i>	42	
		<i>lugens</i>	2	
		<i>poepigii</i>	1	
		sp.	1	
	Callitrichidae	<i>Callimico</i>	<i>goeldi</i>	12
	Cebidae	<i>Cebus</i>	<i>albifrons</i>	136
			<i>apella</i>	131
			<i>capucinus</i>	229
			<i>libidinosus</i>	121
			<i>capucinus</i>	229
			<i>olivaceus</i>	87
			<i>sciureus</i>	232
<i>albinasus</i>			9	
Pitheciidae	<i>Chiropotes</i>	<i>satanas</i>	47	
		<i>monachus</i>	10	
	<i>Pithecia</i>	<i>pithecia</i>	26	
			Total	2,760

Table 3d Primate and primate-outgroup sample examined by TM, categorized by species (Strepsirrhines, Dermopterans)*

Clade	Family	Genus	Species	Specimens examined (n)	
Strepsirrhine	Daubentoniidae	<i>Daubentonia</i>	<i>madagascariensis</i>	2	
		Indriidae	<i>Propithecus</i>	<i>coquereli</i>	1
	<i>coronatus</i>			2	
	<i>deckenii</i>		2		
	<i>diadema</i>		6		
	<i>edwardsi</i>		4		
	<i>holomelas</i>		1		
	<i>verreauxi</i>		1		
	Lemuridae		<i>Eulemur</i>	<i>albifrons</i>	1
				<i>collaris</i>	1
				<i>fulvus</i>	15
		<i>macaco</i>		5	
		<i>mongoz</i>		4	
		<i>rubriventer</i>		4	
		<i>rufus</i>		7	
		sp.		1	
		<i>Hapalemur</i>	<i>griseus</i>	10	
			<i>Lemur</i>	<i>catta</i>	13
			<i>Varecia</i>	<i>rubra</i>	1
	Lorisidae	<i>Arctocebus</i>	<i>variegata</i>	12	
<i>aureus</i>			2		
<i>calabarensis</i>			3		
			Total	98	
Dermoptera	Cynocephalidae	<i>Cynocephalus</i>	<i>volans</i>	20	
		<i>Galeopterus</i>	<i>variegatus</i>	83	
			Total	103	
GRAND TOTAL				4,134	

*All specimens examined by TM are held at the National Museum of Natural History in Washington, D.C. Not all specimens examined are at the appropriate ontogenetic stage to assess dental eruption sequence. A full list of specimens used to assess dental eruption sequence is available in Chapter 3, Table 14

Table 4 Primate and primate-outgroup sample from the literature, by major clade*

Clade	Families (n)	Genera from the literature (n)
Catarrhine	5	11
Platyrrhine	3	5
Strepsirrhine	5	11
Tarsiiforme	1	1
Adapiforme	1	1
Plesiadapiforme	1	1
Scandentia	2	2
Total	18	32

*References for data collected from the literature are available in Table 6

Table 5 Primate and primate-outgroup sample from the literature, by family*

Clade	Family	Genera from the literature (n)	Species from the literature (n)
Catarrhine	Cercopithecidae	6	6
	Gorillidae	1	1
	Hominidae	1	1
	Hylobatidae	1	1
	Panidae	1	1
	Pongidae	1	1
	Total	11	11
Platyrrhine	Aotidae	1	1
	Atelidae	1	1
	Pitheciidae	3	3
	Total	5	5
Strepsirrhine	Archaeolemuridae†	1	2
	Indriidae	1	1
	Lemuridae	4	4
	Lorisidae	4	4
	Megaladapidae†	1	1
	Total	11	12
Tarsiiforme	Tarsiidae	1	1
	Total	1	1
Adapiforme†	Adapidae†	1	1
	Total	1	1
Plesiadapiforme†	Plesiadapidae†	1	1
	Total	1	1
Scandentia	Ptilocercidae	1	1
	Tupaiaidae	1	1
	Total	2	2
TOTAL		32	33

*References for data collected from the literature are available in Table 6

Table 6 References for the primate dental eruption sequences from the literature

Clade	Family	Genus	Species	Reference	
Catarrhine	Cercopithecidae	<i>Cercopithecus</i>	<i>aethiops</i>	Swindler 2002	
		<i>Macaca</i>	<i>mulatta</i>	Schwartz et al. 2005	
		<i>Nasalis</i>	<i>larvatus</i>	Harvati 2000	
		<i>Papio</i>	<i>hamadryas</i>	Schwartz et al. 2005	
		<i>Procolobus</i>	<i>verus</i>	Swindler 2002	
		<i>Semnopithecus</i>	<i>entellus</i>	Schwartz et al. 2005	
	Gorillidae	<i>Gorilla</i>	<i>gorilla</i>	Schwartz et al. 2005	
	Hominidae	<i>Homo</i>	<i>sapiens</i>	Schwartz et al. 2005	
Panidae	<i>Pan</i>	<i>paniscus</i>	Schwartz et al. 2005		
Pongidae	<i>Pongo</i>	<i>pygmaeus</i>	Schwartz et al. 2005		
Platyrrhine	Aotidae	<i>Aotus</i>	<i>trivirgatus</i>	Schwartz et al. 2005	
	Atelidae	<i>Brachyteles</i>	<i>arachnoides</i>	Henderson 2007	
	Pitheciidae	<i>Cacajao</i>	<i>calvus</i>	Henderson 2007	
		<i>Callicebus</i>	<i>donacophius</i>	Henderson 2007	
		<i>Chiropotes</i>	<i>satanas</i>	Henderson 2007	
Strepsirrhine	Archaeolemuridae†	<i>Archaeolemur</i> †	sp. cf. <i>edwardsi</i> †	Schwartz et al. 2005	
			<i>majori</i> †	Schwartz et al. 2005	
			<i>Hadropithecus</i> †	sp.	Schwartz et al. 2005
	Indriidae	<i>Avahi</i>	sp.	Godfrey et al. 2003	
	Lemuridae	<i>Eulemur</i>	<i>fulvus</i>	Schwartz et al. 2005	
			<i>catta</i>	Schwartz 1975	
			<i>mongoz</i>	Schwartz 1975	
			<i>Lepilemur</i>	<i>mustelinus</i>	Schwartz 1975
			Lorisidae	<i>Loris</i>	<i>tardigradus</i>
	<i>Nycticebus</i>	<i>bengalensis</i>		Schwartz 1975	
	<i>Perodicticus</i>	<i>potto</i>		Schwartz 1975	
	Megaladapidae†	<i>Megaladapis</i> †	sp.	Schwartz et al. 2005	
	Tarsiiforme	Tarsiidae	<i>Tarsius</i>	<i>bancanus</i>	Guthrie and Frost 2011
Adapiforme†	Adapidae†	<i>Adapis</i> †	<i>parisiensis</i> †	Smith 2000	
Plesiadapiforme†	Plesiadapidae†	<i>Acidomomys</i> †	<i>hebeticus</i> †	Bloch et al. 2002	
Scandentia	Ptilocercidae	<i>Ptilocercus</i>	<i>lowii</i>	Butler 1980, Dirks et al. 2010	
	Tupaiaidae	<i>Tupaia</i>	<i>glis</i>	Schwartz et al. 2005; Shigehara 1980	

2.4 Evolution of the artiodactyls

Artiodactyls are a large clade of hooved, terrestrial mammals with more than 200 species (Geisler et al. 2007, Hassanin et al. 2012), nested paraphyletically within Artiodactyla (Geisler et al. 2007). Artiodactyls have a global distribution, are almost exclusively herbivorous, and have a significant impact on their local ecosystems (Vrba and Schaller 2000a). Additionally, many artiodactyl species are habitat specialists that are strongly affected by environmental change (e.g., Vrba and Schaller 2000a, Brooks et al. 2001, Buzan et al. 2013). With the exception of some suiformes, artiodactyls are obligate herbivores, and many families have evolved specialized feeding techniques including a dependency on bacterial fermentation (Vrba and Schaller 2000a). As grazers consuming large quantities of plant matter and grasses, artiodactyls play significant roles in ecosystems and on their local ecologies (Owen-Smith et al. 2010), and foraging and grazing by artiodactyls has been linked to vegetation changes in composition, succession sequence, and density (e.g., Molvar et al. 1993, Bowyer 1997).

2.4.1 The earliest artiodactyls

Artiodactyls evolved approximately 70 MA in Eurasia (Hassanin et al. 2012). The geographic origin of artiodactyls is not known precisely, as fossil artiodactyls have been recovered in Asia, Europe, and North America, all dated to the early Eocene (~ 55 MA; Theodor et al. 2007). These early artiodactyls were small-bodied and have been lumped taxonomically as Dichobunidae (McKenna and Bell 1997), or alternatively, divided in two families, Diacodexidae and Dichobunidae (Theodor et al. 2007). The fossil record of Ruminantia spans Asia and North America and extends to approximately 55 MA (Métais and Vislobokova 2007; Theodor et al. 2007). While artiodactyls are rare in the early Eocene, a presumed morphological radiation led to a diversity of body types by the middle Eocene (Theodor et al. 2007). Since the Eocene, Artiodactyla have diversified to include more than 200 extant terrestrial taxa as well as the cetaceans (Geisler et al. 2007, Hassanin et al. 2012).

2.4.2 Domestication of artiodactyls

Artiodactyls represent the mammalian clade most heavily domesticated by humans, and include pigs, cows, sheep, goats, and llamas (Vrba and Schaller 2000a). The impact that artiodactyls have had in human history is unrivaled by any other mammalian group in terms of economics and agriculture, as well as in impact on the environment (Gentry 2000). Domesticated artiodactyls serve as the largest source of farmed meat, milk, skins, and wools globally (Gentry 2000). Overall, as a paraphyletic clade, artiodactyls share many features including life history, diet, and a generalized body plan (Vrba and Schaller 2000a). Many artiodactyls also share an ancestral dental formula with teeth in all four dental classes (i.e., molars, premolars, incisors, and canines in some groups), similar to primates (Hillson 2005), and they are well-sampled in the fossil record.

2.5 Description of the artiodactyl sample

I examined postcanine dental eruption sequence in 81 genera and 100 species, spanning 10 families of Artiodactyla. All extant terrestrial families of Artiodactyla are represented by the

specimens examined for this study. A detailed summary of the artiodactyls examined by TM is presented below by family (Table 7), and by genus (Table 8). All examined specimens are held in the collections of the Museum of Vertebrate Zoology, Berkeley, California (n=852) or the National Museum of Natural History, Washington, D.C. (n=3,925, Table 8). The methods used in examination are described in Chapter 3.

Table 7 Artiodactyls examined by TM, by family

Clade	Family	Genera (n)	Species (n)
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

Table 8a Artiodactyls examined by TM, by genus (Antilocapridae, Bovidae)*

Family	Genus	Specimens examined at MVZ (n)	Specimens examined at NMNH (n)
Antilocapridae	<i>Antilocapra</i>	48	NA
Bovidae	<i>Aepyceros</i>	5	64
	<i>Alcelaphus</i>	NA	131
	<i>Ammotragus</i>	20	17
	<i>Antidorcas</i>	7	28
	<i>Antilope</i>	5	17
	<i>Bison</i>	32	NA
	<i>Bos</i>	10	NA
	<i>Boselaphus</i>	3	8
	<i>Bubalus</i>	NA	44
	<i>Budorcas</i>	NA	20
	<i>Capra</i>	NA	69
	<i>Cephalophus</i>	NA	105
	<i>Connochaetes</i>	NA	60
	<i>Damaliscus</i>	NA	91
	<i>Gazella</i>	NA	105
	<i>Hemitragus</i>	3	11
	<i>Hippotragus</i>	NA	67
	<i>Kobus</i>	NA	200
	<i>Litocranius</i>	3	27
	<i>Madoqua</i>	5	118
	<i>Naemorhedus</i>	NA	33
	<i>Neotragus</i>	NA	28
	<i>Nilgiritragus</i>	NA	1
	<i>Oreamnos</i>	27	50
	<i>Oreotragus</i>	1	32
	<i>Oryx</i>	20	1
	<i>Ourebia</i>	9	71
	<i>Ovibos</i>	4	53
	<i>Ovis</i>	186	NA
	<i>Pantholops</i>	NA	3
	<i>Pelea</i>	NA	1
	<i>Procapra</i>	NA	16
	<i>Pseudois</i>	NA	28
	Total	388	1,499

Table 8b Artiodactyls examined by TM, by genus (Bovidae, Camelidae, Cervidae, Giraffidae)*

Family	Genus	Specimens examined at MVZ (n)	Specimens examined at NMNH (n)
Bovidae	<i>Raphicerus</i>	NA	124
	<i>Redunca</i>	NA	84
	<i>Rupicapra</i>	NA	40
	<i>Saiga</i>	7	NA
	<i>Sigmoceros</i>	NA	28
	<i>Sylvicapra</i>	NA	124
	<i>Syncerus</i>	NA	84
	<i>Taurotragus</i>	NA	40
	<i>Tetracerus</i>	NA	1
	<i>Tragelaphus</i>	NA	121
Camelidae	<i>Camelus</i>	2	15
	<i>Lama</i>	NA	58
	<i>Vicugna</i>	8	28
Cervidae	<i>Alces</i>	NA	162
	<i>Axis</i>	2	31
	<i>Blastoceros</i>	NA	10
	<i>Capreolus</i>	4	37
	<i>Cervus</i>	94	NA
	<i>Dama</i>	2	24
	<i>Elaphodus</i>	NA	24
	<i>Elaphurus</i>	8	NA
	<i>Hippocamelus</i>	NA	8
	<i>Hydropotes</i>	NA	35
	<i>Mazama</i>	30	200
	<i>Muntiacus</i>	NA	120
	<i>Odocoileus</i>	100	NA
	<i>Ozotoceros</i>	NA	12
	<i>Pudu</i>	8	11
	<i>Rangifer</i>	41	200
	<i>Rucervus</i>	NA	25
<i>Rusa</i>	NA	181	
Giraffidae	<i>Giraffa</i>	18	32
	<i>Okapia</i>	NA	6
Total		324	1,865

Table 8c Artiodactyls examined by TM, by genus (Hippopotamidae, Moschidae, Suidae, Tayassuidae, Tragulidae)*

Family	Genus	Specimens examined at MVZ (n)	Specimens examined at NMNH (n)
Hippopotamidae	<i>Hexaprotodon</i>	NA	15
	<i>Hippopotamus</i>	15	32
Moschidae	<i>Moschus</i>	NA	24
Suidae	<i>Babyrousa</i>	NA	36
	<i>Hylochoerus</i>	NA	4
	<i>Phacochoerus</i>	12	107
	<i>Potamochoerus</i>	NA	27
	<i>Sus</i>	58	NA
Tayassuidae	<i>Catagonus</i>	4	7
	<i>Pecari</i>	50	NA
	<i>Tayassu</i>	NA	91
Tragulidae	<i>Hyemoschus</i>	1	7
	<i>Moschiola</i>	NA	11
	<i>Tragulus</i>	NA	200
Total		140	561
GRAND TOTAL		852	3,925

*All specimens examined by TM are held at the Museum of Vertebrate Zoology in Berkeley, California, and the National Museum of Natural History in Washington, D.C. Not all specimens examined are at the appropriate ontogenetic stage to assess dental eruption sequence. A full list of specimens used to assess dental eruption sequence is available in Chapter 3, Table 23

2.6 Summary of the sample used in this study

I examined $n=4,134$ primates and primate-outgroup specimens, and $n=4,777$ artiodactyls, spanning 10 families in each clade. A total of 103 primate and 100 artiodactyl species are represented in this examination. I also gathered data on $n=31$ primate species from the literature. The total sample size of specimens examined for this study is $N=8,911$ and includes taxa from the majority of primate and artiodactyl families. As discussed in the next chapter, not all examined specimens are at the appropriate ontogenetic stage to be included in the assessment of dental eruption sequence. The methods, the full sample of specimens used to determine dental eruption sequence, and the distribution of dental eruption sequences across extant primates and artiodactyls are described in Chapter 3.

CHAPTER 3:

Survey of dental eruption sequence in extant primates and artiodactyls

3.1 Overview

Following a description of materials (Chapter 2), this chapter describes the methods used to assess dental eruption sequence in mammals, with specific notes on variation in methods used for primates versus artiodactyls. The description of methods is accompanied by figures demonstrating different dental eruption sequences as assessed in this study. I also performed a test of intraspecific variation in dental eruption sequence in one primate and one artiodactyl species, the results of which are presented below. Following this, I detail a complete breakdown of all specimens used to determine dental eruption sequence in this study, along with information about sex. All dental eruption sequences determined in this study, from my examination and from the literature, are presented in this chapter. Specific attention is given to taxa that deviate from the predominant dental eruption sequence in their clade. With the distribution of dental eruption sequences presented in this chapter, Chapter 4 tests the relationship between dental eruption sequence and life history (Hypothesis 1, Schultz's Rule), and tests for phylogenetic signal in dental eruption sequence and other life history and body size traits (Hypothesis 2).

3.2 Methods of assessing dental eruption sequence

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, I restricted my study to the functional grinding teeth in herbivores, the postcanine dentition (premolars and molars). The premolars, unlike the molars, have a deciduous complement in heterodont mammals (e.g., Osborn and Crompton 1973, Järvinen et al. 2009) and are the replacement teeth of the postcanine dentition. Following Schultz's Rule, which states that the replacement teeth erupt earlier relative to the permanent teeth in long-lived species, I focused on the relationship between eruption of the premolars and the molars for this study. I visually examined specimens across ontogenetic stages. Because the third molar is always the last molar to erupt in primates and artiodactyls (e.g., Swindler 2002, Hillson 2005), I focused on the relative eruption sequence of the premolars (PM) and the third molar (M3) in primates. Eruption sequence for the primates is defined as either having the third molar erupt after the premolars (Figure 1), or vice versa. In some species of primate, there is significant variation in whether the third molar or one of the premolars erupts last. These primate species are categorized as variable.

The number and morphology of premolars vary across artiodactyls, and I defined eruption sequence slightly differently for artiodactyls than for primates. For artiodactyls, I focused specifically on the relationship between the third molar and the fourth premolar, noting eruption sequence as either the third molar erupting before the fourth premolar, or vice versa (Figure 2). When eruption of the fourth premolar and the third molar seemed to be at the same stage in multiple specimens, the dental eruption sequence for the genus was scored as simultaneous (Figure 2, C). At least two occurrences of eruption sequence for each genus were required to confidently assess the relationship between eruption of the premolars and the third molar, with some exceptions.

I examined eruption sequence in both the maxilla and mandible of each specimen where available, and I use generalized dental notations in this dissertation (e.g. M3 is third molar) unless I am discussing particular mandibular or maxillary teeth of a specimen (e.g. M₃ is mandibular third molar). While I found no difference in eruption sequence between maxilla and mandible in the majority of cases, I did note that eruption tends to occur earlier in the mandible than in the maxilla of an individual.

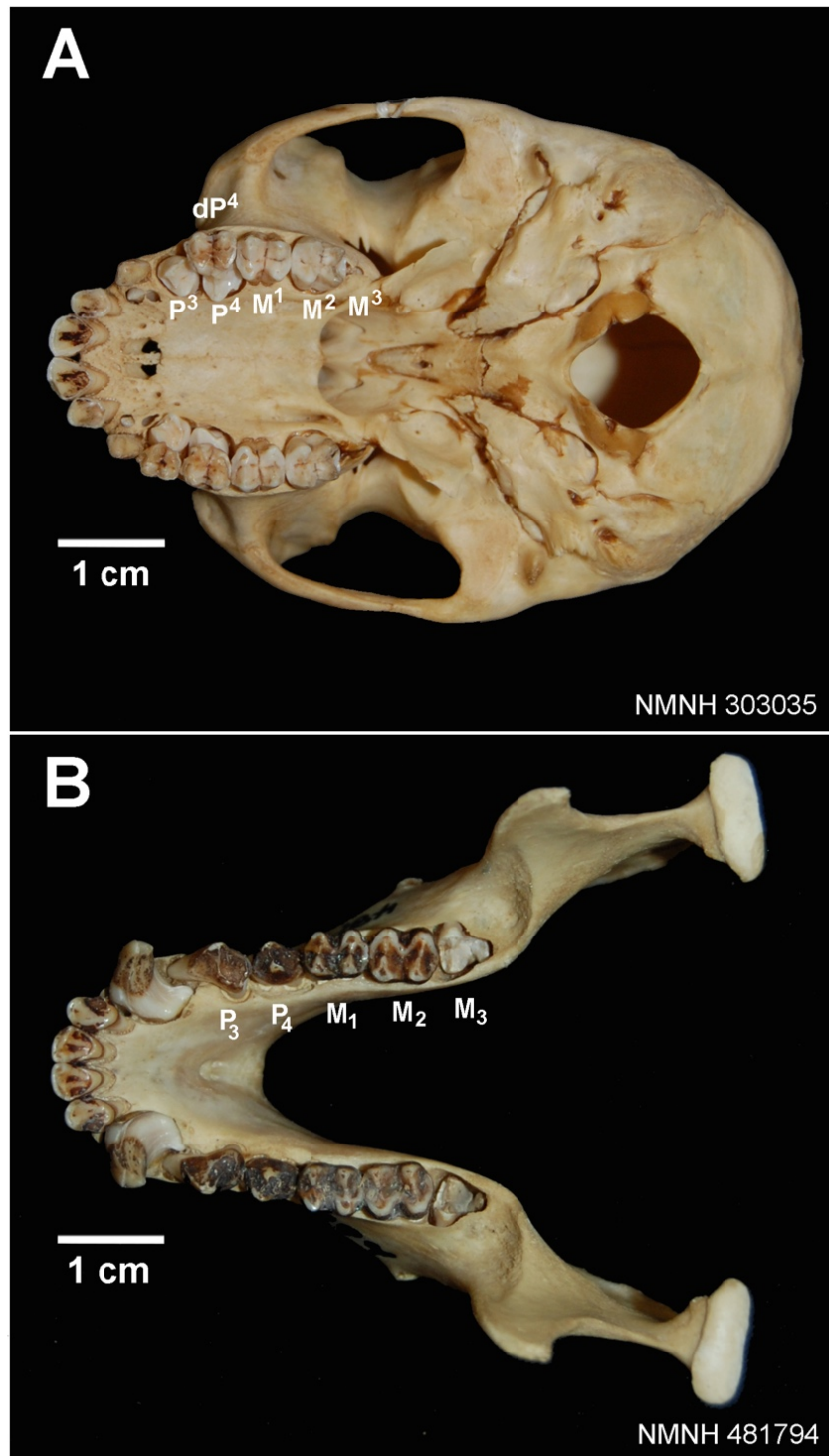


Figure 1 Examples of eruption sequence in primates. M is molar, P is premolar, d is deciduous, and the number denotes tooth number, e.g., dP⁴ is maxillary deciduous premolar 4, A) Eruption of the M³ last in *Trachypithecus phayrei*. Note that the M³ is barely visible in the crypt while P⁴ is well on the way to replacing dP⁴, B) Eruption of the M₃ last in *Ptilocolobus badius*. Note that the M₃ has not yet fully erupted while the P₄ is erupted and in occlusion

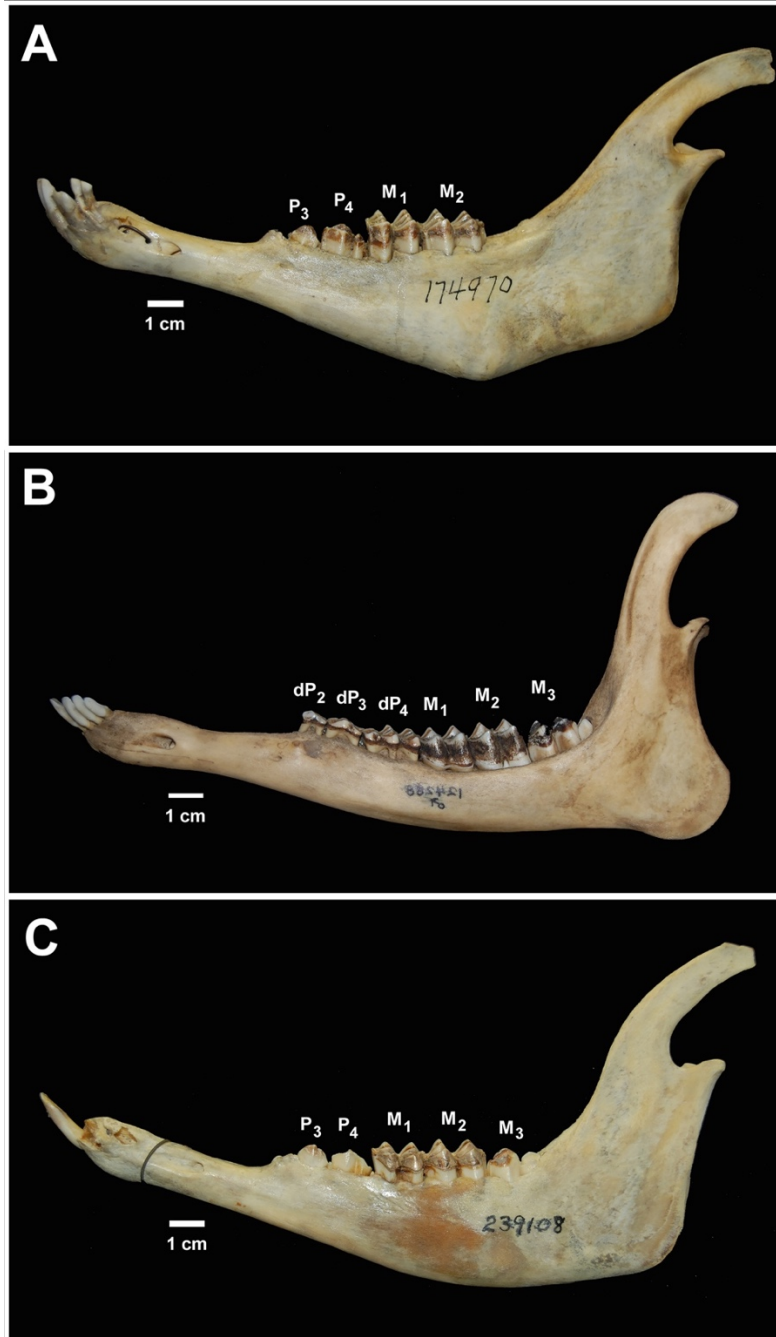


Figure 2 Examples of eruption sequence in artiodactyls. Figure modified from Monson and Hlusko (2016). M is molar, P is premolar, d is deciduous, and the number denotes tooth number, e.g., dP₄ is mandibular deciduous premolar 4. All views are lateral/buccal, A) Eruption of the M₃ last in *Capra caucasica*. Note that the M₃ has only begun to erupt while the P₄ and P₃ are almost completely erupted, B) Eruption of the P₄ after the M₃ in *Odocoileus hemionus*. Image is mirrored for consistency. Note that the M₃ is almost fully erupted and in occlusion while the deciduous premolars, including dP₄, are still in place with no signs of the permanent premolars erupting, C) Simultaneous eruption of M₃ and P₄ in *Oreamnos americanus*. Note that the M₃ and P₄ are both in the process of erupting

3.3 Dental eruption sequences in primates

I was able to definitively assess dental eruption sequence in 22 primate genera and 45 primate species. I also culled dental eruption sequence data from the literature for an additional 30 genera and 31 species, bringing the total number of primate genera and primate species sampled to $n=52$ and $n=76$ respectively (Table 9-13). This sample spans all major clades of primates. I also compiled data on three outgroup species to primates, through investigation at the NMNH (*Galeopterus*, $n=8$), and from the literature (*Ptilocercus lowii*, *Tupaia glis*).

There were some genera for which only one specimen was available at the correct ontogenetic sequence to evaluate dental eruption sequence. In Primates, these genera are *Allenopithecus*, *Pygathrix*, and *Pithecia* (Table 10). Overall, the specimens sampled here provide data for three categories of postcanine dental eruption sequence in primates: 1) the third molar erupts last, 2) one of the premolars erupts last, 3) there is intraspecific variation in whether the third molar or one of the premolars erupts last.

3.3.1 Atypical dental eruption sequences in haplorhines

For the majority of haplorhines, the third molar is the last postcanine tooth to erupt. However, a few species of catarrhine share a dental eruption sequence with the strepsirrhines, where one of the premolars erupts after the third molar. Two species of colobine (*Presbytis hosei* and *Semnopithecus entellus*), and two species of platyrrhine (*Aotus trivirgatus* and *Pithecia monachus*) have this rare dental eruption sequence. Three other platyrrhines (*Alouatta palliata*, *Callimico goeldii*, and *Saimiri sciureus*), and one colobine (*Presbytis melalophos*), exhibit variation in dental eruption sequence, with some specimens erupting the third molar last, and others erupting the premolars after the third molar. With the exception of *Presbytis*, which is discussed in the section on intraspecific variation in dental eruption sequence in primates (3.3.4.D), all of the haplorhine genera with a strepsirrhine-like eruption sequence are discussed in greater detail below.

3.3.1.A *Semnopithecus*

Semnopithecus is a langur genus with a generalized ecology, occupying ranges from desert to high elevation, with both arboreal and terrestrial tendencies (Oppenheimer 1977, Nowak 1999). According to molecular data, *Semnopithecus* and *Presbytis* diverged approximately 10 MA (Pozzi et al. 2014), and fossil *Semnopithecus* specimens have been recovered from Pliocene and Pleistocene deposits of the Indian subcontinent (Jablonski 2002).

Semnopithecus entellus has a dental eruption sequence where one or more of the premolars erupt after the M3, a rare sequence in anthropoids. In the past, *S. entellus* was considered to be a species of *Presbytis* (e.g., Oppenheimer 1977), a genus that I found to be considerably variable in this study, but *S. entellus* has since been awarded its own genus (Eudey 1987, Nowak 1999).

Schultz (1935) originally described a dental eruption sequence for *Pygathrix*, a genus closely related to *Semnopithecus*, where the M3 erupts before one or more of the premolars, comparable to *S. entellus* in this study. I was only able to assess dental eruption sequence in a single specimen of *Pygathrix*, in which I found that the M3 erupts last, contrary to Schultz's (1935) report. However, due to small sample sizes for *Pygathrix* in my study, as well as in

Schultz's (1935) study, it is possible that there is variation in this genus. Because Schultz (1935) only discusses his primate sample at the generic level, it is also possible that shifts in taxonomy over the last 80 years have led to some confusion about the precise taxonomic group sampled.

Overall, several colobine species exhibit a unique dental eruption sequence, or intraspecific variation in dental eruption sequence. Other researchers have also noted that the molars of some colobines, particularly the second molar, erupt relatively early compared to other catarrhines (Harvati 2000, Harvati and Frost 2007). Harvati (2000) noted that *Presbytis* in particular is unique among the colobines in having the earliest eruption of the molars relative to the anterior dentition, as well as relative to the premolars. Harvati (2000) also notes that in some specimens of *Procolobus*, and possibly *Colobus*, the M3 can erupt before the premolars. However, I found no evidence for the M3 erupting before the premolars in *Colobus* here, although one specimen of *C. angolensis* (NMNH 237325) was verging on simultaneous eruption of the M₃ and P₄ in the mandible. Harvati and Frost (2007) also report early eruption of the M2 relative to the anterior dentition in Miocene *Mesopithecus*, arguing that the trait, present in extant colobines, has been present in some colobines at least since the late Miocene (Schultz 1935, Harvati 2000). There is not a good understanding of the relationship between early eruption of the M2 and the M3 (and it is not the focus of this study). However, further work may clarify any possible correlation between eruption timing of the molars relative to each other, as well as relative to the anterior dentition.

3.3.1.B *Aotus*

Aotus and *Callimico* are sister taxa with a deep divergence from the other platyrrhines represented in this study. *Aotus*, the night monkey, is a New World monkey found throughout Central and South America and the only genus in family Aotidae (Groves 1989, 2005), although there is significant disagreement about the taxonomy and phylogenetic placement of this group (Nowak 1999, Goodman et al. 2001). Aotidae is estimated to have diverged from other platyrrhines approximately 20-25 MA (e.g., Schneider and Sampaio 2015), and fossil specimens of *Aotus* have been recovered from the Miocene of Colombia, dated to approximately 12-15 MA (Setoguchi and Rosenberger 1987, Hartwig and Meldrum 2002). *Aotus* is a small arboreal monkey, with a mixed diet of fruits, nuts, flower, gums, bark, small vertebrates, etc., and is known for its excellent vision at night (Mittermeier and Coimbra-Filho 1977, Nowak 1999). In this study, *Aotus* is one of the few anthropoid species that erupts the third molar before the premolars. This dental eruption sequence has been confirmed in other studies (e.g., Henderson 2007).

3.3.1.C *Pithecia*

Like *Aotus*, *Pithecia* is a genus of small, arboreal New World monkey found in many areas throughout South America (Nowak 1999). The diet of *Pithecia* includes fruits, berries and seeds, leaves, flowers, honey, and small vertebrates (Nowak 1999). Taxonomic controversy has resulted in reclassification of *Pithecia* from Cebidae (Nowak 1999) to Atelidae (Fleagle and Tejedor 2002), to a member of its own family, Pitheciidae, the taxonomic designation followed here (Opazo et al. 2006). Recent molecular estimates have dated the divergence of *Pithecia* from *Cacajao* and *Chiropotes* to the Miocene, approximately 10-13 MA. No fossils of *Pithecia* have yet been recovered, but several fossil genera, including *Homunculus*, have been dated to the

early Miocene and attributed to subfamily Pitheciinae (Fleagle and Tejedor 2002). Like *Aotus*, the dental eruption sequence of *Pithecia*, where the third molar erupts before the premolars, has been confirmed in other studies (e.g. Henderson 2007).

3.3.2 Atypical dental eruption sequences in strepsirrhines

Among the strepsirrhines, there are several species that have a dental eruption sequence that deviates from the norm. Of the strepsirrhines sampled here, 70% of the species erupt one of the premolars after the M3. However, four lemuriform genera deviate from this dental eruption sequence: *Lepilemur*, *Lemur*, *Propithecus*, and *Avahi*. Both *Propithecus* and *Avahi* erupt the M3 after the premolars, while *Lepilemur* and *Lemur* exhibit variation in dental eruption sequence. Those taxa that vary from the dominant dental eruption sequence in their clades are discussed in greater detail below.

3.3.2.A Lemuriformes

Among the strepsirrhines, only *Propithecus*, *Avahi*, and *Lemur catta* have an eruption sequence where the M3 erupts after the premolars. However, contrasting reports in the literature suggest that there may be more variation in dental eruption sequence in *Lemur catta* than was seen in this study (e.g. Schwartz 1975, Swindler 2002). *Lepilemur mustelinus*, a sister taxon to *Propithecus* and *Avahi*, also exhibits variation in dental eruption sequence. Together, *Lepilemur*, *Propithecus*, and *Avahi* form a clade that diverged from other lemurs approximately 41 MA (Yoder and Yang 2004) and further diverged in the early Miocene, approximately 17 MA (Masters et al. 2013).

3.3.3 Test of intraspecific variation in dental eruption sequence

In order to assess the level of intraspecific variation in dental eruption sequence in primates, I looked at every single specimen available for the majority of primate genera held at the National Museum of Natural History (n=4,033). Based on this examination, and based on the sample of 193 primate specimens for which I confidently assessed dental eruption sequence, there are either variable or non-variable dental eruption sequences. Non-variable taxa have a consistent dental eruption sequence where either one of the premolars, or the third molar, erupts last in the postcanine dentition. Variable taxa have regular, intraspecific variation in dental eruption sequence, insomuch that it can be classified as a phenotype. In every case classified as exhibiting intraspecific variation in this study, more than 30% of the specimens examined exhibited a non-dominant dental eruption sequence and/or intra-individual dental eruption sequence (see Tables 16 to 18). Species with variation in dental eruption sequence are marked in Table 9 as ‘Variation’.

As a full test of intraspecific variation among taxa that have a consistent, seemingly invariable, dental eruption sequence, I examined every specimen of *Cebus* at the NMNH (n=849) and took detailed notes on postcanine eruption sequence. Of the n=849 *Cebus* specimens, n=62 are in the process of erupting one or more of the postcanine teeth. All specimens included have erupted both the M1 or M2, but the premolars and/or M3 are still unerupted. These 62 specimens span seven species of *Cebus*, as well as one hybrid species listed as *Cebus nigrurus* x *libidinosus*. In order to assess dental eruption sequence, I scored each postcanine tooth based on stage of

eruption. In this scoring system, a score of 0 means the tooth is unerupted, a score of 1 means the tooth is in the process of erupting and is visible above the superior edge of the mandibular corpus when viewed laterally but is not fully erupted, and a score of 2 means the tooth is fully erupted and in occlusion. Within the sample of n=62 *Cebus*, no specimen erupts the third molar before the premolars (Table 15). The average scores for the entire sample support a dental eruption sequence of M1, M2, [P4, P3, P2], M3. The premolars are listed in brackets due to observed variation within species (e.g., female *Cebus capucinus* specimens NMNH 306828 and NMNH 291230). Both the average and median of the sample support that the M3 erupts last in all species of *Cebus*.

While I found no evidence of intra- or interspecific variation in postcanine dental eruption sequence of *Cebus*, several other primate species do exhibit intraspecific variation in eruption sequence (*Alouatta palliata*, *Callimico goeldii*, *Saimiri sciureus*, and *Presbytis melalophos*). These species are discussed in greater detail below along with summaries of dental eruption sequence as assessed in these species.

3.3.4 Intraspecific variation in primate dental eruption sequence

Among the catarrhines sampled in this study, four species are highly variable in dental eruption sequence of the postcanine teeth: *Alouatta palliata*, *Callimico goeldii*, *Saimiri sciureus*, and *Presbytis femoralis*. Both *Alouatta* and *Presbytis* have other species that show no variation in dental eruption sequence, although greater sample sizes could further resolve to what degree variation may or may not exist in the dental eruption sequences of these sister species, particularly in *Presbytis*. Likewise, a larger sample of *Callimico* would resolve the level of intraspecific variation seen in this taxa. However, the sample sizes for *Alouatta* and *Saimiri* are large enough to state with confidence that there is considerable intraspecific variation in dental eruption sequence, as well as intra-individual variation.

3.3.4.A *Alouatta*

Alouatta is a genus of New World monkey, commonly known as the howler monkey, found extensively throughout Central and South America (Nowak 1999). *Alouatta* is one of the largest of the New World monkeys and is heavily dependent on leaf foliage (Nowak 1999). Unique to primates, and the source of their common name, *Alouatta* has evolved an enlarged hyoid bone and derived mandibular morphology that allow the genus to vocalize at greater volumes than other primates (Nowak 1999). The genus is estimated to have diverged from other platyrrhines approximately 16 MA (Cortés-Ortiz et al. 2003). Although fossils of *Alouatta* have yet to be recovered, several specimens of *Stirtonia* have been attributed to tribe Alouattini and are morphologically similar to extant *Alouatta*. *Stirtonia* is a South American Miocene New World monkey known from dental remains as well as a partial mandible, partial maxilla and premaxilla, and partial palate with associated frontal (Hartwig and Meldrum 2002).

I was able to assess dental eruption sequence in three species of *Alouatta* using a total of 27 specimens that are at the appropriate ontogenetic stage. Two of the species (*A. pigra* and *A. seniculus*) have the dominant anthropoid dental eruption sequence where the M3 erupts after the premolars (n=14). In contrast, *A. palliata* shows considerable variation in sequence (Table 16). Within *A. palliata*, n=9 erupt the third molar after the premolars, n=3 erupt the premolars after the third molar, and n=2 have a different sequence between maxilla and mandible (marked by a

D for mandible, and an X for maxilla, Table 16). In contrast, there is no variation in dental eruption sequence in either *A. pigra* or *A. seniculus*. Examples of this interspecific and intra-individual variation are shown in Figure 3. Henderson (2007) also noted some variation, or at least the possibility of simultaneous eruption, in the mandible of *Alouatta*, although without elaboration.

3.3.4.B *Callimico*

As the only genus in family Callitrichidae that has third molars, *Callimico* is the only species of callitrichid sampled for this study. The presence of third molars in *Callimico* is a trait that some researchers believe to be an evolutionary reversal or secondary derivation within the family (e.g., Scott 2015). I examined two specimens of *Callimico* at the National Museum of Natural History that show the eruption of the third molar and the premolars (NMNH 399073 and NMNH 464993). In one specimen, the third molar erupts after the premolars, but in the other, the fourth premolar erupts before the third molar, and as a consequence, I marked the dental eruption sequence of this species as variable. It is unclear if there is any relationship between intraspecific variation in dental eruption sequence and the evolutionary history of the loss (and potential secondary derivation) of third molars in family Callitrichidae. A larger sample size and more thorough examination of *Callimico* may clarify the level of intraspecific variation in dental eruption sequence in this group.

3.3.4.C *Saimiri*

The sister taxon of *Aotus*, *Saimiri* diverged from other platyrrhines in the Miocene approximately 17 MA (Schneider and Sampaio 2015). In this study, *Saimiri* exhibits both intraspecific and intra-individual variation in dental eruption sequence (Table 17). In his original study, Schultz (1935) noted intra-individual variation in dental eruption sequence among *Saimiri* specimens, and he concludes that *Saimiri* erupts the M3 last, but only in the mandible. In contrast, Henderson (2007) reports that the M3 erupts after the premolars in both the maxilla and the mandible among a sample of n=25 *Saimiri*, primarily comprised of specimens from species *S. sciureus*. In this study, I found significant variation in dental eruption sequence in genus *Saimiri*. Many of the specimens I examined at the NMNH exhibit intra-individual variation, where the M3 erupts last in the maxilla only, and the M3 either erupts simultaneously with, or before, the premolars in the mandible (e.g specimens NMNH 397817, NMNH 397816, NMNH 397802, NMNH 397803).

3.3.4.D *Presbytis*

Presbytis is an Asian colobine endemic to islands in Southeast Asia, primarily in Indonesia (Nowak 1999). Species of *Presbytis*, collectively called langurs, are diurnal and arboreal, subsisting on a diet of predominantly fruits, seeds, and foliage (Medway 1970, Bennett and Davies 1994, Nowak 1999). *Presbytis* is one of the most diverse primate genera, with 11 species (Groves 2001), the result of a massive radiation over the last 7 MA (Barry et al. 1987, Meyer et al. 2011), likely driven by climatic and geological changes along the Sunda Shelf (e.g., Lohman et al. 2011).

In this study, *Presbytis* exhibits considerable variation in dental eruption sequence across the genus (Table 18). Of the four species for which I was able to establish dental eruption sequence, two erupt the third molar after the premolars (*P. frontata* and *P. potenziani*), one erupts the third molar before one or more of the premolars (*P. hosei*), and one species exhibits intraspecific variation in dental eruption sequence (*P. melalophos*). Six specimens of *Presbytis hosei* confirm the dental eruption sequence of the species where the third molar erupts before one or more of the premolars (Table 18). I was only able to find three specimens of *Presbytis melalophos* at the appropriate ontogenetic stage to assess dental eruption sequence, and they show two different sequences: NMNH 115503 shows eruption of the third molar after the premolars, but NMNH 86897 shows eruption of the fourth premolars after the third molars. A larger sample size will provide greater clarity about the extent of intraspecific variation in *Presbytis melalophos*.

Presbytis has been noted to be unique in several aspects of craniodental morphology, including covariation of the skull (TM's unpublished data) and teeth (Willis and Swindler 2004, Grieco et al. 2013). Some researchers have proposed that the genus may represent a dwarfed lineage derived from *Trachypithecus*-like ancestors (Jablonski 1998, Jablonski and Tyler 1999, Frazier 2011). I discuss the possible implications of changes in body size for the evolution of dental eruption sequence in greater detail in the discussion (Chapter 7).

3.3.5 Summary of primate dental eruption sequences

Of this large sample of primates, n=55 species erupt the third molar after the premolars, n=21 erupt one of the premolars after the third molar, and n=4 species show variation in dental eruption sequence. A preliminary assessment of the distribution of dental eruption sequences strongly suggests a phylogenetic signal. Of the n=62 anthropoid (catarrhine + platyrrhine) species sampled here, n=55 erupt the M3 after the premolars. In contrast, n=7 of the n=10 extant strepsirrhine species sampled here erupt one of the premolars after the M3. The exceptional anthropoid taxa that erupt one or more of the premolars after the M3 are *Semnopithecus entellus*, *Aotus trivirgatus*, *Pithecia monachus*, and *Presbytis hosei*. Additionally, three anthropoid taxa exhibit intraspecific variation in dental eruption sequence: *Alouatta palliata*, *Saimiri sciureus*, and *Presbytis femoralis*. The data for *A. trivirgatus* and *S. entellus* were taken from the literature, but TM collected the dental eruption sequences for *P. hosei*, *P. monachus*, and all of the taxa exhibiting intraspecific variation. Among the strepsirrhines, *Lemur catta*, *Propithecus diadema*, and *Avahi* sp. are unique in erupting the M3 after the premolars. The data for *L. catta* and *Avahi* were taken from the literature, but the eruption sequence for *P. diadema* was collected by TM during this study.

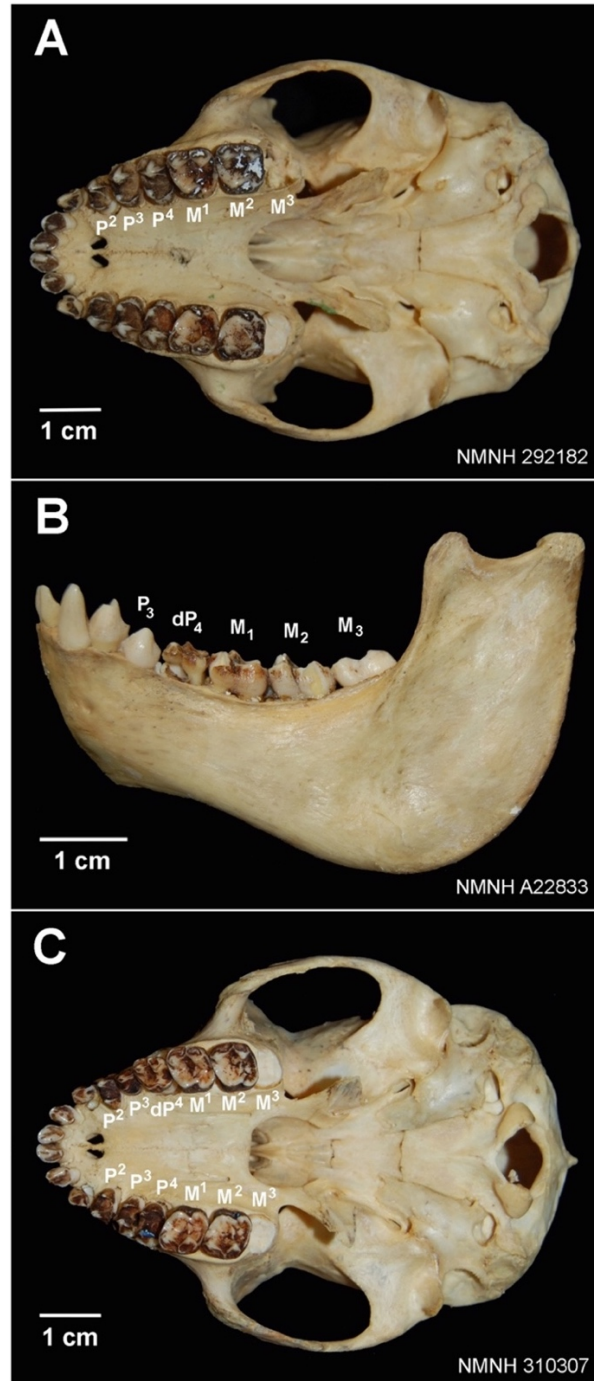


Figure 3 Examples of variation in dental eruption sequence in *Alouatta*. M is molar, P is premolar, d is deciduous, and the number denotes tooth number, e.g., dP₄ is mandibular deciduous premolar 4, A) Eruption of the M³ last in *A. pigra* (palatal view). Note that the M³ is in the crypt while the premolars are fully erupted and in occlusion, B) Eruption of the M₃ before the P₄ in the mandible of *A. palliata* (lateral/buccal view). Note that the M₃ is fully erupted while the P₄ has not yet pushed the crown of dP₄ out of place, C) Intra-individual variation in dental eruption sequence in *A. palliata* (palatal view). Note that the right P⁴ is fully erupted while the left dP⁴ has not yet been shed

Table 9a Primate and primate-outgroup dental eruption sequences as assessed by TM (Catarrhines)*

Clade	Family	Genus	Species	PM before M3		
Catarrhine	Cercopithecidae	<i>Allenopithecus</i>	<i>nigroviridis</i>	YES		
			<i>Cercocebus</i>	<i>agilis</i>	YES	
		<i>torquatus</i>		YES		
		<i>Colobus</i>		<i>angolensis</i>	YES	
				<i>guereza</i>	YES	
				<i>polykomos</i>	YES	
				<i>satanas</i>	YES	
				<i>vellerosus</i>	YES	
				<i>Erythrocebus</i>	<i>patas</i>	YES
				<i>Lophocebus</i>	<i>albigena</i>	YES
				<i>Miopithecus</i>	<i>ogouensis</i>	YES
		<i>Piliocolobus</i>	<i>badius</i>	YES		
		<i>Presbytis</i>	<i>frontata</i>	YES		
			<i>hosei</i>	NO		
			<i>melalophos</i>	VARIATION		
			<i>potenziani</i>	YES		
			<i>Pygathrix</i>	<i>nemaeus</i>	YES	
			<i>Rhinopithecus</i>	<i>roxellana</i>	UNDETERMINED	
		<i>Semnopithecus</i>	<i>entellus</i>	UNDETERMINED		
			<i>johnii</i>	UNDETERMINED		
			<i>priam</i>	UNDETERMINED		
			<i>schistaceus</i>	UNDETERMINED		
			<i>vetulus</i>	UNDETERMINED		
			sp.	UNDETERMINED		
			<i>Trachypithecus</i>	<i>cristatus</i>	YES	
				<i>phayrei</i>	YES	
		Hylobatidae	<i>Hylobates</i>	<i>agilis</i>	YES	
				<i>hoolock</i>	YES	
				<i>klossii</i>	YES	
				<i>lar</i>	YES	
<i>muelleri</i>	YES					
<i>pileatus</i>	YES					
sp.	YES					

Table 9b Primate and primate-outgroup dental eruption sequences as assessed by TM
(Catarrhines (cont.), Platyrrhines, Strepsirrhines, Dermopters)*

Clade	Family	Genus	Species	PM before M3		
Catarrhine	Cercopithecidae	<i>Nomascus</i>	<i>concolor</i>	UNDETERMINED		
			<i>gabriellae</i>	UNDETERMINED		
			<i>leucogenys</i>	UNDETERMINED		
			<i>siki</i>	UNDETERMINED		
Platyrrhine	Atelidae	<i>Symphalangus</i>	<i>syndactylus</i>	YES		
		<i>Alouatta</i>	<i>palliata</i>	VARIATION		
			<i>pigra</i>	YES		
			<i>seniculus</i>	YES		
		<i>Ateles</i>	<i>ater</i> (sp.)	YES		
			<i>belzebuth</i>	YES		
			<i>fusciceps</i>	YES		
			<i>geoffroyi</i>	YES		
		Callitrichidae	<i>Lagothrix</i>	<i>lagotricha</i>	YES	
				Cebidae	<i>Callimico</i>	goeldii
	<i>Cebus</i>				<i>albifrons</i>	YES
					<i>apella</i>	YES
					<i>capucinus</i>	YES
					<i>apella</i> + <i>libidinosus</i>	YES
					<i>olivaceus</i>	YES
		<i>Saimiri</i>	<i>sciureus</i>	VARIATION		
	Pitheciidae	<i>Chiropotes</i>	<i>albinasus</i>	UNDETERMINED		
<i>satanas</i>			UNDETERMINED			
<i>Pithecia</i>			<i>monachus</i>	NO		
Strepsirrhine	Daubentoniidae	<i>Daubentonia</i>	<i>madagascariensis</i>	UNDETERMINED		
	Indriidae	<i>Propithecus</i>	<i>diadema</i>	YES		
	Lemuridae	<i>Eulemur</i>	<i>fulvus</i>	UNDETERMINED		
			<i>Hapalemur</i>	<i>griseus</i>	UNDETERMINED	
			<i>Lemur</i>	<i>catta</i>	UNDETERMINED	
			<i>Varecia</i>	<i>variegata</i>	NO	
	Lorisidae	<i>Arctocebus</i>	<i>aureus</i>	UNDETERMINED		
			<i>calabarensis</i>	UNDETERMINED		
			sp.	UNDETERMINED		
Dermoptera	Cynocephalidae	<i>Galeopterus</i>	<i>variegatus</i>	NO		

* PM is premolars, M3 is third molar

Table 10a Primate and primate-outgroup dental eruption sequences (Catarrhines)*

Clade	Family	Genus	Species	Sample size (n)	PM after M3	M3 after PM	Variation	
Catarrhine	Cercopithecoidea	<i>Allenopithecus</i>	<i>nigroviridis</i>	1		X		
			<i>agilis</i>	1		X		
			<i>torquatus</i>	11		X		
		<i>Cercopithecus</i>	<i>aethiops</i>	literature			X	
			<i>angolensis</i>	1		X		
		<i>Colobus</i>	<i>guereza</i>	4		X		
			<i>polykomos</i>	1		X		
			<i>satanas</i>	1		X		
			<i>vellerosus</i>	1		X		
			<i>patas</i>	3		X		
			<i>albigena</i>	2		X		
	<i>mulatta</i>		literature		X			
	<i>Erythrocebus</i>	<i>Lophocebus</i>	<i>ogouensis</i>	3		X		
			<i>larvatus</i>	literature		X		
		<i>Nasalis</i>	<i>hamadryas</i>	literature		X		
			<i>badius</i>	3		X		
		<i>Ptilocolobus</i>	<i>frontata</i>	1		X		
			<i>hosei</i>	6		X		
		<i>Presbytis</i>	<i>melalophos</i>	3			X	
			<i>potenziani</i>	2			X	
			<i>verus</i>	literature			X	
		<i>Procolobus</i>	<i>Pygathrix</i>	<i>nemaeus</i>	1		X	
	<i>entellus</i>			literature		X		
	<i>Semnopithecus</i>					X		
	Total				45	2	21	1

Table 10b Primate and primate-outgroup dental eruption sequences (Catarrhines (cont.), Platyrrhines)*

Clade	Family	Genus	Species	Sample size (n)	PM after M3	M3 after PM	Variation
Catarrhine	Cercopithecoidea	<i>Trachypithecus</i>	<i>cristatus</i>	2		X	
			<i>phayrei</i>	1		X	
	Gorillidae	<i>Gorilla</i>	<i>gorilla</i>	literature		X	
			<i>sapiens</i>	literature		X	
	Hylobatidae	<i>Hylobates</i>	<i>agilis</i>	2		X	
			<i>hoolock</i>	1		X	
			<i>klossii</i>	2		X	
			<i>lar</i>	4		X	
			<i>muelleri</i>	4		X	
			<i>pileatus</i>	2		X	
	Panidae	<i>Pan</i>	sp.	2		X	
			<i>syndactylus</i>	2		X	
			<i>paniscus</i>	literature		X	
			<i>pygmaeus</i>	literature		X	
Aotidae	<i>Aotus</i>	<i>trivirgatus</i>	literature		X		
		<i>palliata</i>	13			X	
Atelidae	<i>Alouatta</i>	<i>pigra</i>	2			X	
		<i>seniculus</i>	12			X	
		<i>ater</i> (sp.)	6			X	
		<i>belzebuth</i>	8			X	
	<i>Ateles</i>	<i>chamek</i>	1			X	
		<i>fusciceps</i>	3			X	
		<i>geoffroyi</i>	10			X	
		Total		77		1	21

Table 10c Primate and primate-outgroup dental eruption sequences (Platyrrhines (cont.), Strepsirrhines)*

Clade	Family	Genus	Species	Sample size (n)	PM after M3	M3 after PM	Variation	
Platyrrhine	Atelidae	<i>Brachyteles</i>	<i>arachnoides</i>	literature		X		
		<i>Lagothrix</i>	<i>lagotricha</i>	3		X		
	Callitrichidae	<i>Callimico</i>	<i>goeldii</i>	2				X
		Cebidae	<i>Cebus</i>	<i>albifrons</i>	13		X	
	<i>apella</i>		21		X			
	<i>capucinus</i>		9		X			
			<i>libidinosus</i>	5		X		
			<i>olivaceus</i>	6		X		
		<i>Saimiri</i>	<i>sciureus</i>	7				X
	Pitheciidae	<i>Cacajao</i>	<i>calvus</i>	literature		X		
		<i>Callicebus</i>	<i>donacophilus</i>	literature		X		
		<i>Chiropotes</i>	<i>satanas</i>	literature		X		
		<i>Pithecia</i>	<i>monachus</i>	1			X	
		<i>Archaeolemuridae</i> †	<i>Archaeolemur</i> †	sp. cf. <i>edwardsi</i> †	literature		X	
Indridae			<i>majori</i> †	literature		X		
		<i>Hadropithecus</i> †	sp.	literature		X		
Lemuridae	<i>Avahi</i>		sp.	literature			X	
	<i>Propithecus</i>	<i>diadema</i>	1			X		
	<i>Eulemur</i>	<i>fulvus</i>	literature		X			
	<i>Lemur</i>	<i>catta</i>	literature			X		
	<i>Lemur</i>	<i>mongoz</i>	literature		X			
Lorisidae	<i>Lepilemur</i>	<i>mustelinus</i>	literature		X			
	<i>Varecia</i>	<i>variegata</i>	3		X			
	<i>Loris</i>	<i>tardigradus</i>	literature		X			
Total				71	9	13	2	

Table 10d Primate and primate-outgroup dental eruption sequences (Strepsirrhines (cont.), Tarsiiformes, Adapiformes, Plesiadapiformes, Dermopterans, Scandentia)*

Clade	Family	Genus	Species	Sample size (n)	PM after M3	M3 after PM	Variation
Strepsirrhine	Lorisidae	<i>Nycticebus</i>	<i>bengalensis</i>	literature	X		
		<i>Perodicticus</i>	<i>potto</i>	literature	X		
	Megaladapidae	<i>Megaladapis</i>	sp.	literature	X		
Tarsiiforme	Tarsiidae	<i>Tarsius</i>	<i>bancanus</i>	literature	X		
Adapiforme†	Adapidae†	<i>Adapis</i> †	<i>parisiensis</i> †	literature	X		
Plesiadapiforme†	Plesiadapidae†	<i>Acidomomys</i> †	<i>hebeticus</i> †	literature	X		
Dermoptera	Cynocephalidae	<i>Galeopterus</i>	<i>variegatus</i>	8	X		
Scandentia	Ptilocercidae	<i>Ptilocercus</i>	<i>lowii</i>	literature	X		
	Tupaiaidae	<i>Tupaia</i>	<i>glis</i>	literature	X		
Total				8	9	0	0
GRAND TOTAL				201	21	55	4

* PM is premolars, M3 is third molar

Table 11 Sample size (genus) of determined dental eruption sequences in primates

Clade	Family	Genus sample size collected by TM (n)	Genus sample size from the literature (n)
Catarrhine	Cercopithecidae	10	6
	Gorillidae	NA	1
	Hominidae	NA	1
	Hylobatidae	2	NA
	Panidae	NA	1
	Pongidae	NA	1
Platyrrhine	Aotidae	NA	1
	Atelidae	3	1
	Callitrichidae	1	NA
	Cebidae	2	NA
	Pitheciidae	1	3
Strepsirrhine	Archaeolemuridae†	NA	2
	Indriidae	1	1
	Lemuridae	1	4
	Lorisidae	NA	3
	Megaladapidae†	NA	1
Tarsiiforme	Tarsiidae	NA	1
Adapiforme†	Adapidae†	NA	1
Plesiadapiforme†	Plesiadapidae†	NA	1
Dermoptera	Cynocephalidae	1	NA
Scandentia	Ptilocercidae	NA	1
	Tupaiaidae	NA	1
Total		22	31

Table 12a Sample size (species) of determined dental eruption sequences in primates (Catarrhines, Platyrrhines)*

Clade	Family	Genus	Species sample size collected by TM (n)	Species sample size from the literature (n)	
Catarrhine	Cercopithecidae	<i>Allenopithecus</i>	1	NA	
		<i>Cercocebus</i>	2	NA	
		<i>Cercopithecus</i>	NA	1	
		<i>Colobus</i>	5	NA	
		<i>Erythrocebus</i>	1	NA	
		<i>Lophocebus</i>	1	NA	
		<i>Macaca</i>	NA	1	
		<i>Miopithecus</i>	1	NA	
		<i>Nasalis</i>	NA	1	
		<i>Papio</i>	NA	1	
		<i>Ptilocolobus</i>	1	NA	
		<i>Presbytis</i>	4	NA	
		<i>Procolobus</i>	NA	1	
		<i>Pygathrix</i>	1	NA	
		<i>Semnopithecus</i>	NA	1	
		<i>Trachypithecus</i>	2	NA	
		Gorillidae	<i>Gorilla</i>	NA	1
		Hominidae	<i>Homo</i>	NA	1
		Hylobatidae	<i>Hylobates</i>	6	NA
	<i>Symphalangus</i>		1	NA	
Panidae	<i>Pan</i>	NA	1		
Pongidae	<i>Pongo</i>	NA	1		
Platyrrhine	Aotidae	<i>Aotus</i>	NA	1	
	Atelidae	<i>Alouatta</i>	3	NA	
		<i>Ateles</i>	4	NA	
		<i>Brachyteles</i>	NA	1	
		<i>Lagothrix</i>	1	NA	
	Callitrichidae	<i>Callimico</i>	1	NA	
	Cebidae	<i>Cebus</i>	5	NA	
		<i>Saimiri</i>	1	NA	
	Pitheciidae	<i>Cacajao</i>	NA	1	
		<i>Callicebus</i>	NA	1	
		<i>Chiropotes</i>	NA	1	
		<i>Pithecia</i>	1	NA	
			Total	42	15

Table 12b Sample size (species) of determined dental eruption sequences in primates (Strepsirrhines, Tarsiiformes, Adapiformes, Plesiadapiformes, Dermoptera, Scandentia)*

Clade	Family	Genus	Species sample size collected by TM (n)	Species sample size from the literature (n)
Strepsirrhine	Archaeolemuridae†	<i>Archaeolemur</i> †	NA	2
		<i>Hadropithecus</i> †	NA	1
	Indriidae	<i>Avahi</i>	NA	1
		<i>Propithecus</i>	1	NA
	Lemuridae	<i>Eulemur</i>	NA	1
		<i>Lemur</i>	NA	1
		<i>Lemur</i>	NA	1
		<i>Lepilemur</i>	NA	1
		<i>Varecia</i>	1	NA
	Lorisidae	<i>Loris</i>	NA	1
		<i>Nycticebus</i>	NA	1
		<i>Perodicticus</i>	NA	1
	Megaladapidae†	<i>Megaladapis</i> †	NA	1
	Tarsiiforme	Tarsiidae	<i>Tarsius</i>	NA
Adapiforme†	Adapidae†	<i>Adapis</i> †	NA	1
Plesiadapiforme†	Plesiadapidae†	<i>Acidomomys</i> †	NA	1
Dermoptera	Cynocephalidae	<i>Galeopterus</i>	1	NA
Scandentia	Ptilocercidae	<i>Ptilocercus</i>	NA	1
	Tupaiaidae	<i>Tupaia</i>	NA	1
		Total	3	17
GRAND TOTAL			45	32

*Not all genera sampled have associated species information

Table 13a Sample collected by TM, breakdown by sex (Catarrhines)

Clade	Family	Genus	Species	Sample size (n)	Male (n)	Female (n)	Unknown sex (n)	
Catarrhine	Cercopithecoidea	<i>Allenopithecus</i>	<i>nigroviridis</i>	1	NA	NA	1	
		<i>Cercocebus</i>	<i>agilis</i>	1	1	NA	NA	
			<i>torquatus</i>	11	2	9	NA	
		<i>Colobus</i>	<i>angolensis</i>	1	1	NA	NA	
			<i>guereza</i>	4	2	2	NA	
			<i>polykomos</i>	1	NA	1	NA	
			<i>satanas</i>	1	NA	1	NA	
			<i>vellerosus</i>	1	NA	1	NA	
			<i>patas</i>	3	3	NA	NA	
			<i>albigena</i>	2	2	NA	NA	
		<i>Miopithecus</i>	<i>ogouensis</i>	3	1	2	NA	
			<i>badius</i>	3	1	1	1	
		<i>Presbytis</i>	<i>frontata</i>	1	NA	1	NA	
			<i>hosei</i>	6	NA	6	NA	
		<i>Pygathrix</i>	<i>melalophos</i>	3	2	NA	1	
			<i>potenziani</i>	2	1	1	NA	
		<i>Trachypithecus</i>	<i>nemaeus</i>	1	NA	1	NA	
			<i>cristatus</i>	2	1	1	NA	
		Hylobatidae	<i>Hylobates</i>	<i>phayrei</i>	1	NA	1	NA
				<i>agilis</i>	2	NA	2	NA
<i>hoolock</i>	1			NA	1	NA		
<i>klossii</i>	2			1	1	NA		
<i>lar</i>	4			1	3	NA		
<i>muelleri</i>	4			2	2	NA		
Total					61	21	37	3

Table 13b Sample collected by TM, breakdown by sex (Catairrhines (cont.), Platyrrhines, Strepsirrhines, Dermoptera)

Clade	Family	Genus	Species	Sample size (n)	Male (n)	Female (n)	Unknown sex (n)	
Catairrhine	Cercopitheciidae	<i>Hylobates</i>	<i>pileatus</i>	2	2	NA	NA	
			sp.	2	1	NA	1	
		<i>Symphalangus</i>	<i>syndactylus</i>	2	1	1	NA	
Platyrrhine	Atelidae	<i>Alouatta</i>	<i>palliata</i>	13	2	11	NA	
			<i>pigra</i>	2	NA	2	NA	
			<i>seniculus</i>	12	7	3	2	
		<i>Ateles</i>	sp. (<i>ater</i>)	6	1	1	4	
			<i>belzebuth</i>	8	4	2	2	
			<i>chamek</i>	1	1	NA	NA	
			<i>fusciceps</i>	3	3	NA	NA	
		<i>Lagothrix</i>	<i>geoffroyi</i>	10	6	2	2	
			<i>lagotricha</i>	3	1	1	1	
			<i>goeldii</i>	2	2	NA	NA	
		Callitrichidae	<i>Cebus</i>	<i>albifrons</i>	13	6	5	2
				<i>apella</i>	21	7	10	4
		Cebidae		<i>capucinus</i>	9	6	2	1
<i>libidinosus</i>	5			3	2	NA		
<i>olivaceus</i>	6			1	4	1		
<i>sciureus</i>	7			1	3	3		
<i>Saimiri</i>	1			NA	NA	1		
Pitheciidae	<i>Pithecia</i>			<i>monachus</i>	1	NA	NA	NA
				<i>diadema</i>	1	1	NA	NA
Strepsirrhine	Indridae	<i>Propithecus</i>	3	NA	NA	3		
		<i>Varecia</i>	8	1	NA	7		
Dermoptera	Cynocephalidae	<i>Galeopterus</i>	8	1	NA	7		
		<i>variegatus</i>	1	1	NA	NA		
Total				140	57	49	34	
GRAND TOTAL				201	78	86	37	

Table 14a Specimen numbers of the primates and primate-outgroups used to assess dental eruption sequence (Catharrhines)*

Family	Genus	Species	Sample size (n)	Specimen numbers
Cercopithecoidea	<i>Allenopithecus</i>	<i>nigroviridis</i>	1	NMNH 300808
	<i>Cercocebus</i>	<i>agilis</i>	1	NMNH 537772
		<i>torquatus</i>	11	NMNH 220370, NMNH 220351, NMNH 220350, NMNH 220372, NMNH 220353, NMNH 220352, NMNH 218842, NMNH 598495, NMNH 270593, NMNH 49720, NMNH 271011
	<i>Cercopithecus</i>	<i>aethiops</i>	NA	literature
	<i>Colobus</i>	<i>angolensis</i>	1	NMNH 237325
		<i>guereza</i>	4	NMNH 163226, NMNH 163263, NMNH 464983, NMNH 522951
		<i>polykomos</i>	1	NMNH 481788
		<i>satanas</i>	1	NMNH 598561
		<i>vellerosus</i>	1	NMNH 477322
	<i>Erythrocebus</i>	<i>patas</i>	3	NMNH 410530, NMNH 410529, NMNH 538311
	<i>Lophocebus</i>	<i>albigena</i>	2	NMNH 452499, NMNH 220089
	<i>Macaca</i>	<i>mulatta</i>	NA	literature
	<i>Miopithecus</i>	<i>ogouensis</i>	3	NMNH 598531, NMNH 220349, NMNH 396195
	<i>Nasalis</i>	<i>larvatus</i>	NA	literature
	<i>Papio</i>	<i>hamadryas</i>	NA	literature
	<i>Ptilocolobus</i>	<i>badius</i>	3	NMNH 381458, NMNH 481794, NMNH 83908
	<i>Presbytis</i>	<i>frontata</i>	1	NMNH 199188
		<i>hosei</i>	6	NMNH 198283, NMNH 198280, NMNH 198285, NMNH 198291, NMNH 198290, NMNH 292560
Total			39	

Table 14b Specimen numbers of the primates and primate-outgroups used to assess dental eruption sequence (Catharrhines (cont.))*

Family	Genus	Species	Sample size (n)	Specimen numbers
Cercopithecoidea	<i>Presbytis</i>	<i>melalophos</i>	3	NMNH 115503, NMNH 86897, NMNH 83408
		<i>potenziani</i>	2	NMNH 121664, NMNH 252314
	<i>Procolobus</i>	<i>verus</i>	NA	literature
		<i>nemaus</i>	1	NMNH 356854
	<i>Pygathrix</i>	<i>entellus</i>	NA	literature
		<i>Semnopithecus</i>		
	<i>Trachypithecus</i>	<i>cristatus</i>	2	NMNH 156311, NMNH 2576835
<i>phayrei</i>		1	NMNH 303035	
Gorillidae	<i>Gorilla</i>			
Hominidae	<i>gorilla</i>	NA	literature	
	<i>sapiens</i>	NA	literature	
Hylobatidae	<i>Hylobates</i>	<i>agilis</i>	2	NMNH 113177, NMNH 143576
		<i>hoolock</i>	1	NMNH 279146
	<i>klossii</i>	2	NMNH 121681, NMNH 121677	
	<i>lar</i>	4	NMNH 111990, NMNH 307763, NMNH 112574, NMNH 083264	
	<i>muelleri</i>	4	NMNH 198271, NMNH 198842, NMNH 198268, NMNH 196779	
	<i>pileatus</i>	2	NMNH 321550, NMNH 347648	
	<i>sp.</i>	2	NMNH 300923, NMNH 395693	
Panidae	<i>Symphalangus</i>			
	<i>Pan</i>	<i>syndactylus</i>	2	NMNH 141163, NMNH 395691
Pongidae	<i>Pan</i>	<i>paniscus</i>	NA	literature
	<i>Pongo</i>	<i>pygmaeus</i>	NA	literature
Total			28	

Table 14c Specimen numbers of the primates and primate-outgroups used to assess dental eruption sequence (Platyrrhines)*

Family	Genus	Species	Sample size (n)	Specimen numbers
Aotidae	<i>Aotus</i>	<i>trivirgatus</i>	NA	literature
Atelidae	<i>Alouatta</i>	<i>palliata</i>	13	NMNH 257357, NMNH 338110, NMNH 315826, NMNH 291963, NMNH 291212, NMNH 291208, NMNH 291209, NMNH 310307, NMNH 171067, NMNH 306823, NMNH 362284, NMNH 266856, NMNH 257358
		<i>pigra</i>	2	NMNH 292201, NMNH 292182
		<i>seniculus</i>	12	NMNH 194351, NMNH 261320, NMNH 44382, NMNH 443747, NMNH 443376, NMNH 372757, NMNH 143148, NMNH 281673, NMNH 281756, NMNH 281758, NMNH 194351, NMNH 261320
	<i>Ateles</i>	<i>ater</i> (sp.)	6	NMNH 63425, NMNH 82746, NMNH 59160, NMNH 397952, NMNH 49712, NMNH A984
		<i>belzebuth</i>	8	NMNH 281811, NMNH 281779, NMNH 281790, NMNH 281083, NMNH 281793, NMNH 281804, NMNH 443226, NMNH 406478
		<i>chamek</i>	1	NMNH 194338
		<i>fusciceps</i>	3	NMNH 362294, NMNH 521041, NMNH 336279
		<i>geoffroyi</i>	10	NMNH A14162, NMNH 315841, NMNH 74671, NMNH 282273, NMNH 292216, NMNH 292214, NMNH 292218, NMNH 284950, NMNH 337699, NMNH 337865
	<i>Brachyteles</i>	<i>arachnoides</i>	NA	literature
	<i>Lagothrix</i>	<i>lagothricha</i>	3	NMNH 282791, NMNH 398460, NMNH 399302
Callitrichidae	<i>Callimico</i>	<i>goeldii</i>	2	NMNH 399073, NMNH 464993
Cebidae	<i>Cebus</i>	<i>albifrons</i>	13	NMNH 281628, NMNH 397962, NMNH 398505, NMNH 398451, NMNH 406438, NMNH 443627, NMNH 398447, NMNH 239665, NMNH 281580, NMNH 281589, NMNH 281594, NMNH 281590, NMNH 281662
Total			73	

Table 14d Specimen numbers of the primates and primate-outgroups used to assess dental eruption sequence (Platyrrhines (cont.), Strepsirrhines)*

Family	Genus	Species	Sample size (n)	Specimen numbers
Cebidae	<i>Cebus</i>	<i>apella</i>	21	NMNH 518303, NMNH 518302, NMNH 547896, NMNH 397941, NMNH 397959, NMNH 240987, NMNH 14220, NMNH 518465, NMNH 518403, NMNH 518408, NMNH 518467, NMNH 518416, NMNH 518408, NMNH 518271, NMNH 518274, NMNH 518402, NMNH 518491, NMNH 518458, NMNH 518511, NMNH 518498, NMNH 518335
		<i>capucinus</i>	9	NMNH 291230, NMNH 25311, NMNH 284774, NMNH 283908, NMNH 283907, NMNH 306828, NMNH 310310, NMNH 283940, NMNH 223389
		<i>libidinosus</i>	5	NMNH 518526, NMNH 518339, NMNH 518522, NMNH 518531, NMNH 518521
		<i>olivaceus</i>	6	NMNH 372768, NMNH 258501, NMNH 406635, NMNH 148742, NMNH 336197, NMNH 296286
	<i>Saimiri</i>	<i>sciureus</i>	7	NMNH 522059, NMNH 522058, NMNH 398685, NMNH 397802, NMNH 397817, NMNH 397816, NMNH 398628
Pitheciidae	<i>Cacajao</i>	<i>calvus</i>	NA	literature
	<i>Callicebus</i>	<i>donacophilus</i>	NA	literature
	<i>Chiropotes</i>	<i>satanas</i>	NA	literature
	<i>Pithecia</i>	<i>monachus</i>	1	NMNH 38498/16606
Archaeolemuridae†	<i>Archaeolemur</i> †	sp. cf. <i>edwardsi</i> †	NA	literature
Total			49	

Table 14e Specimen numbers of the primates and primate-outgroups used to assess dental eruption sequence (Strepsirrhines (cont.), Tarsiiformes, Adapiformes, Plesiadapiformes, Dermoptera, Scandentia)*

Family	Genus	Species	Sample size (n)	Specimen numbers
Archaeolemuridae†	<i>Archaeolemur</i> †	<i>majori</i> †	NA	literature
	<i>Hadropithecus</i> †	sp.	NA	literature
Indriidae	<i>Avahi</i>	sp.	NA	literature
	<i>Propithecus</i>	<i>diadema</i>	1	NMNH 63348
Lemuridae	<i>Eulemur</i>	<i>fulvus</i>	NA	literature
	<i>Lemur</i>	<i>catta</i>	NA	literature
	<i>Lemur</i>	<i>mongoz</i>	NA	literature
	<i>Lepilemur</i>	<i>mustelinus</i>	NA	literature
	<i>Varecia</i>	<i>variegata</i>	3	NMNH 84381, NMNH 84383, NMNH 503392
Lorisidae	<i>Loris</i>	<i>tardigradus</i>	NA	literature
	<i>Nycticebus</i>	<i>bengalensis</i>	NA	literature
	<i>Perodicticus</i>	<i>potto</i>	NA	literature
Megaladapidae†	<i>Megaladapis</i> †	sp.	NA	literature
Tarsiidae	<i>Tarsius</i>	<i>bancanus</i>	NA	literature
Adapidae†	<i>Adapis</i> †	<i>parisiensis</i> †	NA	literature
Plesiadapidae†	<i>Acidomomys</i> †	<i>hebeiticus</i> †	NA	literature
Cynocephalidae	<i>Galeopterus</i>	<i>variegatus</i>	8	NMNH 121854, NMNH 253411, NMNH 154600, NMNH 258871, NMNH 317119, NMNH 300827, NMNH 300826, NMNH 197203
Ptilocercidae	<i>Ptilocercus</i>	<i>lowii</i>	NA	literature
Tupaiaidae	<i>Tupaia</i>	<i>glis</i>	NA	literature
GRAND TOTAL		Total	12	
			201	

* NMNH is National Museum of Natural History, † indicates an extinct taxon

Table 15a Test of intraspecific variation in *Cebus**

ID	Species	Sex	P2	P3	P4	M1	M2	M3
NMNH 281628	<i>C. albifrons</i>	M	0	1	2	2	2	0
NMNH 397962	<i>C. albifrons</i>	M	2	2	2	2	2	1
NMNH 398505	<i>C. albifrons</i>	U	2	2	2	2	2	1
NMNH 398451	<i>C. albifrons</i>	U	2	2	2	2	2	1
NMNH 406438	<i>C. albifrons</i>	F	2	2	2	2	2	1
NMNH 443627	<i>C. albifrons</i>	M	2	2	2	2	2	1
NMNH 398447	<i>C. albifrons</i>	M	2	2	2	2	2	1
NMNH 239665	<i>C. albifrons</i>	M	2	2	2	2	2	1
NMNH 281580	<i>C. albifrons</i>	F	2	2	2	2	2	1
NMNH 281589	<i>C. albifrons</i>	F	2	2	2	2	2	1
NMNH 281594	<i>C. albifrons</i>	M	2	2	2	2	2	1
NMNH 281590	<i>C. albifrons</i>	F	2	2	2	2	2	1
NMNH 281622	<i>C. albifrons</i>	F	2	2	2	2	2	1
NMNH 518298	<i>C. apella</i>	F	0	0	0	2	2	0
NMNH 547896	<i>C. apella</i>	F	1	2	2	2	2	0
NMNH 518449	<i>C. apella</i>	M	0	0	0	2	2	0
NMNH 518448	<i>C. apella</i>	M	0	0	0	2	2	0
NMNH 396012	<i>C. apella</i>	M	1	0	0	2	2	0
NMNH 545872	<i>C. apella</i>	F	1	2	1	2	2	0
NMNH 397941	<i>C. apella</i>	F	2	2	2	2	2	1
NMNH 240987	<i>C. apella</i>	M	2	2	2	2	2	1
NMNH 283907	<i>C. capucinus</i>	M	1	2	2	2	2	0
NMNH 306828	<i>C. capucinus</i>	F	1	2	2	2	2	0
NMNH 336197	<i>C. capucinus</i>	U	2	1	1	2	2	0
NMNH 315836	<i>C. capucinus</i>	M	2	1	1	2	2	0
NMNH A 14220	<i>C. capucinus</i>	U	2	2	2	2	2	1
NMNH 291230	<i>C. capucinus</i>	F	2	2	2	2	2	1
NMNH A 25311	<i>C. capucinus</i>	U	2	2	2	2	2	1
NMNH 284774	<i>C. capucinus</i>	M	2	2	2	2	2	1
NMNH 283908	<i>C. capucinus</i>	M	2	2	2	2	2	1
NMNH 310310	<i>C. capucinus</i>	M	2	2	2	2	2	1
NMNH 283940	<i>C. capucinus</i>	M	2	2	2	2	2	1
NMNH 296286	<i>C. capucinus</i>	F	2	2	2	2	2	1
NMNH 223389	<i>C. capucinus</i>	M	2	2	2	2	2	1
NMNH 518467	<i>C. libidinosus</i>	M	0	1	2	2	2	0

Table 15b Test of intraspecific variation in *Cebus*, continued*

ID	Species	Sex	P2	P3	P4	M1	M2	M3
NMNH 518465	<i>C. libidinosus</i>	F	2	2	2	2	2	1
NMNH 518408	<i>C. libidinosus</i>	M	2	2	2	2	2	1
NMNH 518416	<i>C. libidinosus</i>	M	2	2	2	2	2	1
NMNH 518408	<i>C. libidinosus</i>	M	2	2	2	2	2	1
NMNH 518271	<i>C. libidinosus</i>	F	2	2	2	2	2	1
NMNH 518274	<i>C. libidinosus</i>	F	2	2	2	2	2	1
NMNH 518429	<i>C. nigrinus</i>	F	0	0	0	2	2	0
NMNH 518313	<i>C. nigrinus</i>	F	0	0	0	2	2	0
NMNH 518463	<i>C. nigrinus</i>	M	2	1	1	2	2	0
NMNH 518335	<i>C. nigrinus</i>	M	2	1	1	2	2	0
NMNH 518403	<i>C. nigrinus</i>	F	2	2	2	2	2	1
NMNH 518491	<i>C. nigrinus</i>	M	2	2	2	2	2	1
NMNH 518458	<i>C. nigrinus</i>	F	2	2	2	2	2	1
NMNH 518511	<i>C. nigrinus</i>	F	2	2	2	2	2	1
NMNH 518498	<i>C. nigrinus</i>	F	2	2	2	2	2	1
NMNH 518526	<i>C. nigrinus</i> x <i>libidinosus</i>	F	2	2	2	2	2	1
NMNH 518399	<i>C. nigrinus</i> x <i>libidinosus</i>	F	2	2	2	2	2	1
NMNH 518522	<i>C. nigrinus</i> x <i>libidinosus</i>	M	2	2	2	2	2	1
NMNH 518531	<i>C. nigrinus</i> x <i>libidinosus</i>	M	2	2	2	2	2	1
NMNH 518521	<i>C. nigrinus</i> x <i>libidinosus</i>	M	2	2	2	2	2	1
NMNH 518402	<i>C. nigrinus</i> x <i>libidinosus</i>	M	2	2	2	2	2	1
NMNH 372768	<i>C. nigrivittatus</i>	M	2	2	2	2	2	1
NMNH 258501	<i>C. nigrivittatus</i>	F	2	2	2	2	2	1
NMNH 406635	<i>C. nigrivittatus</i>	F	2	2	2	2	2	1
NMNH 148742	<i>C. nigrivittatus</i>	F	2	2	2	2	2	1
NMNH 518303	<i>C. xanthosternos</i>	M	2	2	2	2	2	1
NMNH 518302	<i>C. xanthosternos</i>	F	2	2	2	2	2	1
	Average		1.69	1.71	1.73	2.00	2.00	0.74
	Median		2	2	2	2	2	1

* NMNH is National Museum of Natural History, F is female, M is male, U is unknown, P2 is second premolar, P3 is third premolar, P4 is fourth premolar, M1 is first molar, M2 is second molar, M3 is third molar

Table 16 Intraspecific variation in dental eruption sequence in *Alouatta**

ID	Species	Sex	M3 before PM	M3 after PM	Simultaneous
NMNH 257357	<i>A. palliata</i>	F		X	
NMNH 362284	<i>A. palliata</i>	F		X	
NMNH 338110	<i>A. palliata</i>	F		X	
NMNH 315826	<i>A. palliata</i>	F		X (X)	X (D)
NMNH 291963	<i>A. palliata</i>	F		X	
NMNH 291212	<i>A. palliata</i>	F		X	
NMNH 291208	<i>A. palliata</i>	M	X (D)	X (X)	
NMNH 291209	<i>A. palliata</i>	F		X	
NMNH 310307	<i>A. palliata</i>	F	X		
NMNH 291176	<i>A. palliata</i>	F		X	
NMNH 171067	<i>A. palliata</i>	F		X	
NMNH A 22833	<i>A. palliata</i>	F	X		
NMNH 306823	<i>A. palliata</i>	F		X	
NMNH 361222	<i>A. palliata</i>	F	X		
NMNH 292201	<i>A. pigra</i>	F		X	
NMNH 292182	<i>A. pigra</i>	F		X	
NMNH 194351	<i>A. seniculus</i>	M		X	
NMNH 261320	<i>A. seniculus</i>	M		X	
NMNH 443382	<i>A. seniculus</i>	M		X	
NMNH 443747	<i>A. seniculus</i>	M		X	
NMNH 443746	<i>A. seniculus</i>	F		X	
NMNH 372757	<i>A. seniculus</i>	M		X	
NMNH 143148	<i>A. seniculus</i>	F(?)		X	
NMNH 281673	<i>A. seniculus</i>	M		X	
NMNH 281756	<i>A. seniculus</i>	M		X	
NMNH 281758	<i>A. seniculus</i>	F		X	
NMNH 261320	<i>A. seniculus</i>	U		X	

* NMNH is National Museum of Natural History, (X) is maxillary, (D) is mandibular, M3 is third molar, PM is premolars, F is female, M is male, (?) indicates uncertainty, U is unknown

Table 17 Intraspecific variation in dental eruption sequence in *Saimiri**

ID	Species	Sex	M3 after PM	M3 before PM	Simultaneous
NMNH 397802	<i>S. sciureus</i>	U		X	
NMNH 397816	<i>S. sciureus</i>	U	X (X)	X (D)	
NMNH 397817	<i>S. sciureus</i>	U	X		
NMNH 398628	<i>S. sciureus</i>	F	X (X)		X (D)
NMNH 398685	<i>S. sciureus</i>	M	X		
NMNH 522058	<i>S. sciureus</i>	F	X		
NMNH 522059	<i>S. sciureus</i>	F	X		

* NMNH is National Museum of Natural History, (X) is maxillary, (D) is mandibular, M3 is third molar, PM is premolars, F is female, M is male, U is unknown

Table 18 Intra- and interspecific variation in dental eruption sequence in *Presbytis**

Specimen ID	Species	Sex	M3 after PM	M3 before PM	Simultaneous
NMNH 199188	<i>P. frontatus</i>	F	X		
NMNH 198283	<i>P. hosei</i>	F		X	
NMNH 198280	<i>P. hosei</i>	F		X	
NMNH 198285	<i>P. hosei</i>	F		X	
NMNH 198290	<i>P. hosei</i>	F		X	
NMNH 198291	<i>P. hosei</i>	F		X	
NMNH 292560	<i>P. hosei</i>	F		X	
NMNH 83408	<i>P. melalophos</i>	U	X		
NMNH 115503	<i>P. melalophos</i>	M	X		
NMNH 86897	<i>P. melalophos</i>	M		X	
NMNH 121664	<i>P. potenziani</i>	M	X		
NMNH 252314	<i>P. potenziani</i>	F	X		

* NMNH is National Museum of Natural History, (X) is maxillary and (D) is mandibular, M3 is third molar, PM is premolars, F is female, M is male, U is unknown

3.4 Dental eruption sequence in artiodactyls

I definitively assessed postcanine eruption sequence in 62 genera and 81 artiodactyl species. Of those, 46 genera have a sequence where the fourth premolar erupts after the third molar, 13 genera have a sequence where the third molar erupts after the fourth premolar, and three genera have a sequence with approximately simultaneous eruption of the fourth premolar and the third molar (Table 19-20). I found four more genera that likely erupt the fourth premolar after the third molar, and one genus that likely erupts the third molar last, but I need a larger sample size to definitively confirm these sequences. I was unable to assess dental eruption sequence in 14 genera based on a lack of available specimens at appropriate ontogenetic stages.

The artiodactyl sample is slightly skewed toward males (Table 22), possibly a product of collection bias. Male artiodactyls are frequently characterized by secondary sex characteristics like horns and antlers that make them desirable hunting trophies. Since many of the artiodactyls sampled were collected more than 50 years ago, it is possible that there was favoritism for male specimens during collection.

A complete list of specimens used to determine dental eruption sequence is available in Table 23. I found no evidence of interspecific variation in dental eruption sequence in artiodactyls. However, there were some artiodactyl genera in which only one specimen was available at the correct ontogenetic sequence to evaluate dental eruption sequence. These genera are *Bos*, *Bubalus*, *Catagonus*, *Hippocamelus*, *Hylochoerus*, *Nilgiritragus*, *Ozotoceros*, *Pelea*, *Phacochoerus*, *Pseudois*, and *Rucervus* (Table 21).

3.4.1 Variation in dental eruption sequence across artiodactyls

In this study, I successfully sampled the breadth of the artiodactyl phylogeny, and my results support a conserved phylogenetic signal. Genera sampled in Camelidae, Hippopotamidae, Suidae, and Tayassuidae all erupt the third molar after the fourth premolar. In contrast, nested within the artiodactyl clade, ruminant families Bovidae, Moschidae, Cervidae, Antilocapridae, and Tragulidae almost exclusively erupt the fourth premolar after the third molar, although there are some exceptions. Of the 52 ruminant genera I examined, 45 erupt the fourth premolar after the third molar. The exceptional genera are *Capra*, *Hemitragus*, *Nilgiritragus*, *Oreamnos*, *Oryx*, *Ourebia*, and *Ovis*.

3.4.1.A Caprinae

Capra, *Hemitragus*, *Nilgiritragus*, and *Ovis* all erupt the third molar after the fourth premolar, uniquely among Ruminantia (Figure 4). These four genera are all part of subfamily Caprinae. Due to small sample sizes, I was unable to definitively 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 third molar after the fourth premolar. 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 2005, 2006). The earliest fossil occurrence of subfamily Caprinae is hypothesized to be *Protoryx enanus* from the middle Miocene of Europe (Köhler 1987, Gentry and Heinzmann 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).

3.4.1.B Simultaneous eruption of the fourth premolar and third molar in artiodactyls

Oryx, *Ourebia*, and *Oreamnos* appear to erupt the fourth premolar and third molar 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 fourth premolar or third molar erupts later in these taxa. *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 third molar after the fourth premolar (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, my data show that subfamily Caprinae is unique among Ruminantia in having a cluster of genera that erupt the third molar after the fourth premolar (*Capra*, *Hemitragus*, *Nilgiritragus*, and *Ovis*), as well as one genus with simultaneous eruption of the third molar and fourth premolar (*Oreamnos*).

3.4.2 Test of intraspecific variation in dental eruption sequence

To assess intraspecific variation in dental eruption sequence, I systematically surveyed all *Ovis* craniodental specimens available at the Museum of Vertebrate Zoology in Berkeley, California (MVZ; *Ovis canadensis* n=176, *Ovis dalli* n=9). For artiodactyls, I 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. My 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 by TM at the MVZ, n=48 are in the process of erupting one or more of the postcanine teeth. This sample is 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, I find no variability in dental eruption sequence. Based on this analysis, I am confident in assuming that my 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 Appendices A (mandibular data) and B (maxillary data).

3.4.3 Summary of artiodactyl dental eruption sequences

I confidently assessed dental eruption sequence in 192 artiodactyl specimens spanning 62 genera and 81 species, and representing 10 artiodactyl families. Giraffidae is the only family for which I was not able to confidently assess dental eruption sequence. Hippopotamidae, Tragulidae, and Camelidae are also represented by small sample sizes. Of these 62 artiodactyl species, n=46 erupt the fourth premolar after the third molar, n=13 erupt the third molar after the fourth premolar, and three species appear to have simultaneous eruption of the fourth premolar and third molar. The dental eruption sequences are clustered by clade, and all of the taxa basal to the ruminants erupt the third molar last. Within Ruminantia, the vast majority of taxa erupt the fourth premolar after the third molar. However, there are some exceptional ruminant taxa that erupt the third molar after the fourth premolar like more basal artiodactyls. In particular, six caprine species erupt the third molar after the fourth premolar, and one caprine species appears to erupt the fourth premolar and third molar simultaneously. Four other bovid species (two genera) also simultaneously erupt the fourth premolar and third molar. All of the cervid species sampled (n=18) erupt the fourth premolar after the third molar with no observed variation. Additional sampling will continue to refine our understanding of dental eruption sequence in artiodactyls and other mammals.

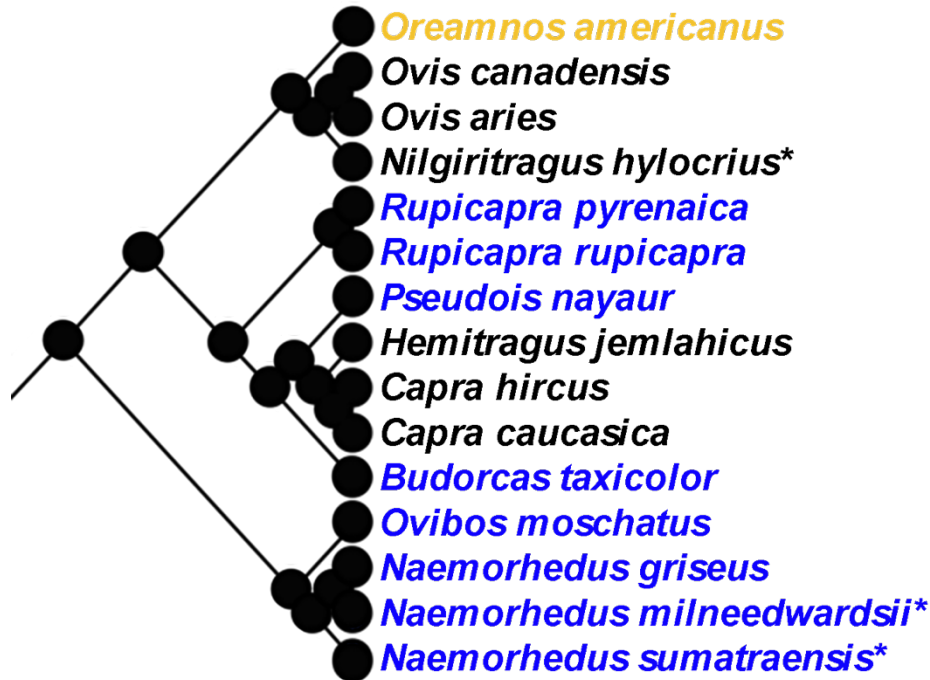


Figure 4 The distribution of dental eruption sequences across subfamily Caprinae. Black indicates that the third molar erupts after the premolars, blue indicates that the fourth premolar erupts after the third molar, and yellow indicates that the third molar and the fourth premolar erupt simultaneously. An asterisk denotes a species with an alternate genus level classification

Table 19a Results of TM's examination of artiodactyl dental eruption sequence

Family	Genus	Species	P4 erupts after M3
Antilocapridae	<i>Antilocapra</i>	<i>americana</i>	YES
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	YES
	<i>Alcelaphus</i>	<i>buselaphus</i>	YES
		<i>lichtensteinii</i>	YES
		<i>lervia</i>	UNDETERMINED
	<i>Ammotragus</i>	<i>lervia</i>	UNDETERMINED
	<i>Antidorcas</i>	<i>marsupialis</i>	YES
	<i>Antilope</i>	<i>cervicapra</i>	UNDETERMINED
	<i>Bison</i>	<i>bison</i>	YES
	<i>Bos</i>	<i>grunniens</i>	YES
	<i>Boselaphus</i>	<i>tragocamelus</i>	UNDETERMINED
	<i>Bubalus</i>	<i>bubalis</i>	YES
	<i>Budorcas</i>	<i>taxicolor</i>	YES
	<i>Capra</i>	<i>caucasica</i>	NO
		<i>hircus</i>	NO
	<i>Cephalophus</i>	<i>weynsi</i>	YES
	<i>Connochaetes</i>	<i>taurinus</i>	YES
	<i>Damaliscus</i>	<i>korrigum</i>	YES
	<i>Gazella</i>	<i>arabica</i>	YES
		<i>bennettii</i>	YES
		<i>dorcas</i>	YES
	<i>Hemitragus</i>	<i>jemlahicus</i>	NO
	<i>Hippotragus</i>	<i>equinus</i>	YES
		<i>niger</i>	YES
	<i>Kobus</i>	<i>ellipsiprymnus</i>	YES
	<i>Litocranius</i>	<i>walleri</i>	YES
	<i>Madoqua</i>	<i>guentheri</i>	YES
		<i>kirkii</i>	YES
	<i>Naemorhedus</i>	<i>griseus</i>	YES
		<i>*C. milneedwardsii</i>	YES
		<i>*C. sumatraensis</i>	YES
<i>Neotragus</i>	<i>pygmaeus</i>	YES	
<i>Nesotragus</i>	<i>moschatus</i>	YES	
<i>Nilgiritragus</i>	<i>hylocrius</i>	YES	
<i>Oreamnos</i>	<i>americanus</i>	SIMULTANEOUS	
<i>Oreotragus</i>	<i>oreotragus</i>	YES	

Table 19b Results of TM's examination of artiodactyl dental eruption sequence, continued

Family	Genus	Species	P4 erupts after M3
Bovidae	<i>Oryx</i>	<i>beisa</i>	SIMULTANEOUS
		<i>dammah</i>	SIMULTANEOUS
		<i>gazella</i>	SIMULTANEOUS
	<i>Ourebia</i>	<i>ourebi</i>	SIMULTANEOUS
	<i>Ovibos</i>	<i>moschatus</i>	YES
	<i>Ovis</i>	<i>aries</i>	NO
		<i>canadensis</i>	NO
	<i>Pantholops</i>	<i>hodgsonii</i>	UNDETERMINED
	<i>Pelea</i>	<i>capreolus</i>	YES
	<i>Procapra</i>	<i>gutturosa</i>	LIKELY
	<i>Pseudois</i>	<i>nayaur</i>	YES
	<i>Raphicerus</i>	<i>campestris</i>	YES
	<i>Redunca</i>	<i>fulvorufula</i>	YES
		<i>redunca</i>	YES
	<i>Rupicapra</i>	<i>pyrenaica</i>	YES
		<i>rupicapra</i>	YES
	<i>Saiga</i>	<i>tatarica</i>	UNDETERMINED
	<i>Sylvicapra</i>	<i>grimmia</i>	YES
	<i>Syncerus</i>	<i>caffer</i>	YES
	<i>Taurotragus</i>	<i>oryx</i>	YES
	<i>Tetracerus</i>	<i>quadricornis</i>	UNDETERMINED
	<i>Tragelaphus</i>	<i>scriptus</i>	YES
	Camelidae	<i>Camelus</i>	<i>bactrianus</i>
<i>Lama</i>		<i>glama</i>	NO
Cervidae	<i>Alces</i>	<i>americanus</i>	YES
	<i>Axis</i>	<i>axis</i>	LIKELY
	<i>Blastocerus</i>	<i>dichotomus</i>	UNDETERMINED
	<i>Capreolus</i>	<i>pygargus</i>	LIKELY
	<i>Cervus</i>	<i>elaphus</i>	YES
	<i>Dama</i>	<i>dama</i>	UNDETERMINED
	<i>Elaphodus</i>	<i>cephalophus</i>	YES
	<i>Elaphurus</i>	<i> davidianus</i>	UNDETERMINED
	<i>Hippocamelus</i>	<i>antisensis</i>	YES
	<i>Hydropotes</i>	<i>inermis</i>	YES
	<i>Mazama</i>	<i>americana</i>	YES
<i>rufina</i>		YES	

Table 19c Results of TM's examination of artiodactyl dental eruption sequence, continued

Family	Genus	Species	P4 erupts after M3
Cervidae	<i>Muntiacus</i>	<i>muntjac</i>	YES
		<i>reevesi</i>	YES
	<i>Odocoileus</i>	<i>hemionus</i>	YES
	<i>Ozotoceros</i>	<i>bezoarticus</i>	YES
	<i>Pudu</i>	<i>mephistophiles</i>	YES
		<i>puda</i>	YES
	<i>Rangifer</i>	<i>tarandus</i>	YES
	<i>Rucervus</i>	<i>eldii</i>	YES
	<i>Rusa</i>	<i>timorensis</i>	YES
<i>unicolor</i>		YES	
Giraffidae	<i>Giraffa</i>	<i>camelopardalis</i>	UNDETERMINED
	<i>Okapia</i>	<i>johnstoni</i>	UNDETERMINED
Hippopotamidae	<i>Hexaprotodon</i>	<i>liberiensis</i>	UNDETERMINED
	<i>Hippopotamus</i>	<i>amphibius</i>	NO
Moschidae	<i>Moschus</i>	<i>berezovskii</i>	YES
Suidae	<i>Babyrousa</i>	<i>babyrussa</i>	NO
		<i>celebensis</i>	NO
	<i>Hylochoerus</i>	<i>meinertzhageni</i>	NO
	<i>Phacochoerus</i>	<i>aethiopicus</i>	NO
	<i>Potamochoerus</i>	<i>porcus</i>	NO
	<i>Sus</i>	<i>scrofa</i>	NO
Tayassuidae	<i>Catagonus</i>	<i>wagneri</i>	NO
	<i>Pecari</i>	<i>tajacu</i>	NO
	<i>Tayassu</i>	<i>pecari</i>	NO
Tragulidae	<i>Hyemoschus</i>	<i>aquaticus</i>	UNDETERMINED
	<i>Moschiola</i>	<i>meminna</i>	LIKELY
	<i>Tragulus</i>	<i>kanchil</i>	YES

Table 20a Artiodactyl dental eruption sequences as assessed by TM*

Family	Genus	Species	N	P4 later	M3 later	Simult.	
Antilocapridae	<i>Antilocapra</i>	<i>americana</i>	2	X			
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	3	X			
	<i>Alcelaphus</i>	<i>buselaphus</i>	3	X			
		<i>lichtensteini</i>	1	X			
	<i>Antidorcas</i>	<i>marsupialis</i>	1	X			
	<i>Bison</i>	<i>bison</i>	4	X			
	<i>Bos</i>	<i>grunniens</i>	1	X			
	<i>Bubalus</i>	<i>bubalis</i>	1	X			
	<i>Budorcas</i>	<i>taxicolor</i>	3	X			
	<i>Capra</i>	<i>caucasica</i>	1			X	
		<i>hircus</i>	2			X	
	<i>Cephalophus</i>	<i>weynsi</i>	2	X			
	<i>Connochaetes</i>	<i>taurinus</i>	3	X			
	<i>Damaliscus</i>	<i>korrigum</i>	4	X			
	<i>Gazella</i>	<i>arabica</i>	1	X			
		<i>bennettii</i>	1	X			
		<i>dorcas</i>	3	X			
	<i>Hemitragus</i>	<i>jemlahicus</i>	2			X	
	<i>Hippotragus</i>	<i>equinus</i>	1	X			
		<i>niger</i>	3	X			
	<i>Kobus</i>	<i>ellipsiprymnus</i>	4	X			
	<i>Litocranius</i>	<i>walleri</i>	6	X			
	<i>Madoqua</i>	<i>guentheri</i>	2	X			
		<i>kirkii</i>	1	X			
	<i>Naemorhedus</i>	<i>griseus</i>	3	X			
		<i>*C. milneedwardsii</i>	1	X			
		<i>*C. sumatraensis</i>	1	X			
	<i>Neotragus</i>	<i>pygmaeus</i>	2	X			
	<i>Nesotragus</i>	<i>moschatus</i>	2	X			
	<i>Nilgiritragus</i>	<i>hylocrius</i>	1			X	
	<i>Oreamnos</i>	<i>americanus</i>	2				X
<i>Oreotragus</i>	<i>oreotragus</i>	5	X				
Total			72	27	4	1	

Table 20b Artiodactyl dental eruption sequences as assessed by TM, continued*

Family	Genus	Species	N	P4 later	M3 later	Simult.	
Bovidae	<i>Oryx</i>	<i>beisa</i>	1			X	
		<i>dammah</i>	1			X	
		<i>gazella</i>	2			X	
	<i>Ourebia</i>	<i>ourebi</i>	4			X	
	<i>Ovibos</i>	<i>moschatus</i>	4	X			
	<i>Ovis</i>	<i>aries</i>	1			X	
		<i>canadensis</i>	5			X	
	<i>Pelea</i>	<i>capreolus</i>	1	X			
	<i>Pseudois</i>	<i>nayaur</i>	1	X			
	<i>Raphicerus</i>	<i>campestris</i>	6	X			
	<i>Redunca</i>	<i>fulvorufula</i>	1	X			
		<i>redunca</i>	1	X			
	<i>Rupicapra</i>	<i>pyrenaica</i>	2	X			
		<i>rupicapra</i>	1	X			
	<i>Sylvicapra</i>	<i>grimmia</i>	4	X			
	<i>Syncerus</i>	<i>caffer</i>	4	X			
	<i>Taurotragus</i>	<i>oryx</i>	3	X			
	<i>Tragelaphus</i>	<i>scriptus</i>	4	X			
	Camelidae	<i>Lama</i>	<i>glama</i>	2		X	
	Cervidae	<i>Alces</i>	<i>americanus</i>	2	X		
<i>Cervus</i>		<i>elaphus</i>	3	X			
<i>Elaphodus</i>		<i>cephalophus</i>	3	X			
<i>Hippocamelus</i>		<i>antisensis</i>	1	X			
<i>Hydropotes</i>		<i>inermis</i>	2	X			
<i>Mazama</i>		<i>americana</i>	3	X			
		<i>rufina</i>	1	X			
		<i>temama</i>	1	X			
Total			64	20	3	4	

Table 20c Artiodactyl dental eruption sequences as assessed by TM, continued*

Family	Genus	Species	N	P4 later	M3 later	Simult.
Cervidae	<i>Muntiacus</i>	<i>muntjac</i>	1	X		
		<i>reevesi</i>	1	X		
	<i>Odocoileus</i>	<i>hemionus</i>	3	X		
	<i>Ozotoceros</i>	<i>bezoarticus</i>	1	X		
	<i>Pudu</i>	<i>mephistophiles</i>	1	X		
		<i>puda</i>	1	X		
	<i>Rangifer</i>	<i>tarandus</i>	4	X		
	<i>Rucervus</i>	<i>eldii</i>	1	X		
	<i>Rusa</i>	<i>timorensis</i>	2	X		
<i>unicolor</i>		1	X			
Hippopotamidae	<i>Hippopotamus</i>	<i>amphibius</i>	2		X	
Moschidae	<i>Moschus</i>	<i>berezovskii</i>	2	X		
Suidae	<i>Babyrousa</i>	<i>babyrussa</i>	1		X	
		<i>celebensis</i>	1		X	
	<i>Hylochoerus</i>	<i>meinertzhageni</i>	1		X	
	<i>Phacochoerus</i>	<i>aethiopicus</i>	3		X	
	<i>Potamochoerus</i>	<i>porcus</i>	3		X	
	<i>Sus</i>	<i>scrofa</i>	17		X	
Tayassuidae	<i>Catagonus</i>	<i>wagneri</i>	1		X	
	<i>Pecari</i>	<i>tajacu</i>	2		X	
	<i>Tayassu</i>	<i>pecari</i>	4		X	
Tragulidae	<i>Tragulus</i>	<i>kanchil</i>	3	X		
Total			56	12	10	NA
GRAND TOTAL			192	59	17	5

* N is specimen sample size, P4 is fourth premolar, M3 is third molar, Simult. is simultaneous. An asterisk denotes a species with alternate genus-level classification. Table modified from Monson and Hlusko (2016)

Table 21 Sample size of determined dental eruption sequences in artiodactyls

Family	Genera (n)	Species (n)	Specimen count (n)
Antilocapridae	1	1	2
Bovidae	36	49	116
Camelidae	1	1	2
Cervidae	13	18	32
Hippopotamidae	1	1	2
Moschidae	1	1	2
Suidae	5	6	26
Tayassuidae	3	3	7
Tragulidae	1	1	3
TOTAL	62	81	192

Table 22a Artiodactyl sample collected by TM, breakdown by sex*

Family	Genus	Species	N	M (n)	F (n)	U (n)	
Antilocapridae	<i>Antilocapra</i>	<i>americana</i>	2	1	1	NA	
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	3	1	1	1	
	<i>Alcelaphus</i>	<i>buselaphus</i>	3	3	NA	NA	
		<i>lichtensteinii</i>	1	NA	1	NA	
	<i>Antidorcas</i>	<i>marsupialis</i>	1	NA	1	NA	
	<i>Bison</i>	<i>bison</i>	4	3	1	NA	
	<i>Bos</i>	<i>grunniens</i>	1	1	NA	NA	
	<i>Bubalus</i>	<i>bubalis</i>	1	1	NA	NA	
	<i>Budorcas</i>	<i>taxicolor</i>	3	NA	3	NA	
	<i>Capra</i>	<i>caucasica</i>	1	1	NA	NA	
		<i>hircus</i>	2	1	1	NA	
	<i>Cephalophus</i>	<i>weynsi</i>	2	1	1	NA	
	<i>Connochaetes</i>	<i>taurinus</i>	3	NA	1	2	
	<i>Damaliscus</i>	<i>korrigum</i>	4	1	3	NA	
	<i>Gazella</i>	<i>arabica</i>	1	1	NA	NA	
		<i>bennettii</i>	1	NA	NA	1	
		<i>dorcas</i>	3	2	1	NA	
	<i>Hemitragus</i>	<i>jemlahicus</i>	2	1	NA	1	
	<i>Hippotragus</i>	<i>equinus</i>	1	NA	1	NA	
		<i>niger</i>	3	2	1	NA	
	<i>Kobus</i>	<i>ellipsiprymnus</i>	4	2	2	NA	
	<i>Litocranius</i>	<i>walleri</i>	6	4	2	NA	
	<i>Madoqua</i>	<i>guentheri</i>	2	2	NA	NA	
		<i>kirkii</i>	1	NA	1	NA	
	<i>Naemorhedus</i>	<i>griseus</i>	3	1	2	NA	
		* <i>C. milneedwardsii</i>	1	1	NA	NA	
		* <i>C. sumatraensis</i>	1	1	NA	NA	
	<i>Neotragus</i>	<i>pygmaeus</i>	2	1	1	NA	
	<i>Nesotragus</i>	<i>moschatus</i>	2	1	1	NA	
	<i>Nilgiritragus</i>	<i>hylocrius</i>	1	1	NA	NA	
	<i>Oreamnos</i>	<i>americanus</i>	2	1	NA	1	
	<i>Oreotragus</i>	<i>oreotragus</i>	5	3	2	NA	
		<i>Oryx</i>	<i>beisa</i>	1	NA	1	NA
			<i>dammah</i>	1	1	NA	NA
	<i>gazella</i>	2	1	NA	1		
Total			76	40	29	7	

Table 22b Artiodactyl sample collected by TM, breakdown by sex, continued*

Family	Genus	Species	N	M (n)	F (n)	U (n)
Bovidae	<i>Ourebia</i>	<i>ourebi</i>	4	4	NA	NA
	<i>Ovibos</i>	<i>moschatus</i>	4	2	NA	2
	<i>Ovis</i>	<i>aries</i>	1	NA	1	NA
		<i>canadensis</i>	5	3	NA	2
	<i>Pelea</i>	<i>capreolus</i>	1	NA	1	NA
	<i>Pseudois</i>	<i>nayaur</i>	1	1	NA	NA
	<i>Raphicerus</i>	<i>campestris</i>	6	4	2	NA
	<i>Redunca</i>	<i>fulvorufula</i>	1	NA	1	NA
		<i>redunca</i>	1	1	NA	NA
	<i>Rupicapra</i>	<i>pyrenaica</i>	2	2	NA	NA
		<i>rupicapra</i>	1	NA	NA	1
	<i>Sylvicapra</i>	<i>grimmia</i>	4	3	1	NA
	<i>Syncerus</i>	<i>caffer</i>	4	1	3	NA
	<i>Taurotragus</i>	<i>oryx</i>	3	2	NA	1
	<i>Tragelaphus</i>	<i>scriptus</i>	4	2	1	1
Camelidae	<i>Lama</i>	<i>glama</i>	2	2	NA	NA
Cervidae	<i>Alces</i>	<i>americanus</i>	2	1	1	NA
	<i>Cervus</i>	<i>elaphus</i>	3	3	NA	NA
	<i>Elaphodus</i>	<i>cephalophus</i>	3	3	NA	NA
	<i>Hippocamelus</i>	<i>antisensis</i>	1	NA	1	NA
	<i>Hydropotes</i>	<i>inermis</i>	2	1	NA	1
	<i>Mazama</i>	<i>americana</i>	3	1	1	1
		<i>rufina</i>	1	NA	1	NA
		<i>temama</i>	1	1	NA	NA
	<i>Muntiacus</i>	<i>muntjac</i>	1	NA	1	NA
		<i>reevesi</i>	1	NA	1	NA
	<i>Odocoileus</i>	<i>hemionus</i>	3	2	NA	1
	<i>Ozotoceros</i>	<i>bezoarticus</i>	1	1	NA	NA
	<i>Pudu</i>	<i>mephistophiles</i>	1	1	NA	NA
		<i>puda</i>	1	NA	1	NA
	<i>Rangifer</i>	<i>tarandus</i>	4	2	2	NA
	<i>Rucervus</i>	<i>eldii</i>	1	1	NA	NA
	<i>Rusa</i>	<i>timorensis</i>	2	2	NA	NA
		<i>unicolor</i>	1	1	NA	NA
	Hippopotamidae	<i>Hippopotamus</i>	<i>amphibius</i>	2	1	NA
Moschidae	<i>Moschus</i>	<i>berezovskii</i>	2	1	NA	1
Total			80	49	19	12

Table 22c Artiodactyl sample collected by TM, breakdown by sex, continued*

Family	Genus	Species	N	M (n)	F (n)	U (n)
Suidae	<i>Babyrousa</i>	<i>babyrussa</i>	1	1	NA	NA
		<i>celebensis</i>	1	NA	1	NA
	<i>Hylochoerus</i>	<i>meinertzhageni</i>	1	NA	1	NA
	<i>Phacochoerus</i>	<i>aethiopicus</i>	3	1	1	1
	<i>Potamochoerus</i>	<i>porcus</i>	3	1	NA	1
	<i>Sus</i>	<i>scrofa</i>	17	11	5	1
Tayassuidae	<i>Catagonus</i>	<i>wagneri</i>	1	NA	NA	1
	<i>Pecari</i>	<i>tajacu</i>	2	NA	NA	2
	<i>Tayassu</i>	<i>pecari</i>	4	2	NA	2
Tragulidae	<i>Tragulus</i>	<i>kanchil</i>	3	2	1	NA
Total			36	18	9	8
GRAND TOTAL			192	107	57	25

*N is specimen sample size, M is male, F is female, U is unknown. An asterisk denotes a species with alternate genus-level classification

Table 23a Specimen numbers of the artiodactyls used to assess dental eruption sequence*

Family	Genus	Species	N	Specimen Numbers
Antilocapridae	<i>Antilocapra</i>	<i>americana</i>	2	MVZ 165925, MVZ 69027
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	3	MVZ 4864, NMNH 368557, NMNH 470199
	<i>Alcelaphus</i>	<i>buselaphus</i>	3	NMNH 161954, NMNH 162995, NMNH 161963
		<i>lichtensteini</i>	1	NMNH 20868
	<i>Antidorcas</i>	<i>marsupialis</i>	1	MVZ 117917
	<i>Bison</i>	<i>bison</i>	4	MVZ 116960, MVZ 44131, MVZ 161219, MVZ 161215
	<i>Bos</i>	<i>grunniens</i>	1	MVZ 55145
	<i>Bubalus</i>	<i>bubalis</i>	1	NMNH 357402
	<i>Budorcas</i>	<i>taxicolor</i>	3	NMNH 258825, NMNH 258655, NMNH 259024
	<i>Capra</i>	<i>caucasica</i>	1	NMNH 174970
		<i>hircus</i>	2	NMNH 328580, NMNH 327097
	<i>Cephalophus</i>	<i>weynsi</i>	2	NMNH 182399, NMNH 164843
	<i>Connochaetes</i>	<i>taurinus</i>	3	NMNH 296156, NMNH 296157, NMNH 181889
	<i>Damaliscus</i>	<i>korrigum</i>	4	NMNH 163000, NMNH 163001, NMNH 181862, NMNH 182411
	<i>Gazella</i>	<i>arabica</i>	1	NMNH 395771
		<i>bennettii</i>	1	NMNH A866
		<i>dorcas</i>	3	NMNH 302304, NMNH 322837, NMNH 319785
	<i>Hemitragus</i>	<i>jemlahicus</i>	2	NMNH 16149, NMNH 105926
<i>Hippotragus</i>	<i>equinus</i>	1	NMNH 164608	
	<i>niger</i>	3	NMNH 163167, NMNH 545318, NMNH 61740	
<i>Kobus</i>	<i>ellipsiprymnus</i>	4	NMNH 164793, NMNH 395850, NMNH 164513, NMNH 164559	
<i>Litocranius</i>	<i>walleri</i>	6	MVZ 126878, NMNH 164031, NMNH 164037, NMNH 164038, NMNH 182062, NMNH 259457	
Total			52	

Table 23b Specimen numbers of the artiodactyls used to assess dental eruption sequence, continued*

Family	Genus	Species	N	Specimen Numbers
Bovidae	<i>Madoqua</i>	<i>guentheri</i>	2	NMNH 299865, NMNH 182050
		<i>kirkii</i>	1	MVZ 124285
	<i>Naemorhedus</i>	<i>griseus</i>	3	NMNH 258692, NMNH 152164, NMNH 199040
		* <i>C. milneedwardsii</i>	1	NMNH 258671
		* <i>C. sumatraensis</i>	1	NMNH 267332
	<i>Neotragus</i>	<i>pygmaeus</i>	2	NMNH 450449, NMNH 450448
		<i>moschatus</i>	2	NMNH 308855, NMNH 367449
	<i>Nilgiritragus</i>	<i>hylocrius</i>	1	MVZ 119567
	<i>Oreamnos</i>	<i>americanus</i>	2	MVZ 93852, MVZ 8335
	<i>Oreotragus</i>	<i>oreotragus</i>	5	MVZ 184211, NMNH 182150, NMNH 314959, NMNH 161988, NMNH 181844
	<i>Oryx</i>	<i>beisa</i>	1	NMNH 182130
		<i>dammah</i>	1	NMNH 449934
		<i>gazella</i>	2	MVZ 4844, NMNH 241366
<i>Ourebia</i>	<i>ourebi</i>	4	NMNH 439826, NMNH 439828, NMNH 155421, NMNH 163246	
	<i>moschatus</i>	4	MVZ 74674, NMNH 291027, NMNH 251408, NMNH 256709	
<i>Ovis</i>	<i>aries</i>	1	MVZ 185197	
	<i>canadensis</i>	5	MVZ 145637, MVZ 61917, MVZ 94723, MVZ 186316, MVZ 70205	
<i>Pelea</i>	<i>capreolus</i>	1	NMNH 469910	
<i>Pseudois</i>	<i>nayaur</i>	1	NMNH 270276	
<i>Raphicerus</i>	<i>campestris</i>	6	NMNH 163032, NMNH 368532, NMNH 368535, NMNH 368546, NMNH 368547, NMNH 368544	
<i>Redunca</i>	<i>fulvorufula</i>	1	NMNH 161994	
	<i>redunca</i>	1	NMNH 164679	
Total			48	

Table 23c Specimen numbers of the artiodactyls used to assess dental eruption sequence, continued*

Family	Genus	Species	N	Specimen Numbers
Bovidae	<i>Rupicapra</i>	<i>pyrenaica</i>	2	NMNH A1859, NMNH 327744
		<i>rupicapra</i>	1	NMNH 174651
	<i>Sylvicapra</i>	<i>grimmia</i>	4	MVZ 118489, NMNH 470183, NMNH 368523, NMNH 429185
		<i>caffer</i>	4	NMNH 220128, NMNH 219060, NMNH 220136, NMNH 220295
	<i>Taurotragus</i>	<i>oryx</i>	3	MVZ 4854, NMNH 122741, NMNH 181860
	<i>Tragelaphus</i>	<i>scriptus</i>	4	NMNH 367403, NMNH 34696*, NMNH 164742, NMNH 470534
	Camelidae	<i>Lama</i>	<i>glama</i>	2
Cervidae	<i>Alces</i>	<i>americanus</i>	2	NMNH 174522, NMNH 267356
		<i>elaphus</i>	3	MVZ 119905, MVZ 57122, MVZ 129718
	<i>Elaphodus</i>	<i>cephalophus</i>	3	NMNH 258557, NMNH 258679, NMNH 258556
		<i>antisensis</i>	1	NMNH 194303
	<i>Hydropotes</i>	<i>inermis</i>	2	NMNH 197890, NMNH 217130
		<i>americana</i>	3	MVZ 136659, NMNH 281440, NMNH 374884
	<i>Mazama</i>	<i>rufina</i>	1	MVZ 124095
		<i>temama</i>	1	NMNH 336233
		<i>muntiac</i>	1	NMNH 300187
	<i>Muntiacus</i>	<i>reevesi</i>	1	NMNH 239596
		<i>hemionus</i>	3	MVZ 17811, MVZ 39922, MVZ 39897
		<i>bezoarticus</i>	1	NMNH 256129
	<i>Odocoileus</i>	<i>mehistophiles</i>	1	NMNH 309044
	<i>Pudu</i>	<i>puda</i>	1	NMNH 583207
	Total			44

Table 23d Specimen numbers of the artiodactyls used to assess dental eruption sequence, continued*

Family	Genus	Species	N	Specimen Numbers	
Cervidae	<i>Rangifer</i>	<i>tarandus</i>	4	MVZ 125628, NMNH 244848, NMNH 290441, NMNH 175720	
	<i>Rucervus</i>	<i>eldii</i>	1	NMNH 588224	
	<i>Rusa</i>	<i>timorensis</i>	2	NMNH 218572, NMNH 218059	
		<i>unicolor</i>	1	NMNH 145369	
Hippopotamidae	<i>Hippopotamus</i>	<i>amphibius</i>	2	MVZ 124269, MVZ 117895	
Moschidae	<i>Moschus</i>	<i>berezovskii</i>	2	NMNH 254799, NMNH 258357	
Suidae	<i>Babyrousa</i>	<i>babyrousa</i>	1	NMNH 258215	
		<i>celebensis</i>	1	NMNH 199893	
	<i>Hylchoerus</i>	<i>meinertzhageni</i>	1	NMNH 268957	
	<i>Phacochoerus</i>	<i>aethiopicus</i>	3	MVZ 4860, NMNH 368513, NMNH 368517	
		<i>porcus</i>	3	NMNH 220138, NMNH 220140	
	<i>Sus</i>	<i>scrofa</i>	17	MVZ 125510, MVZ 116963, MVZ 140031, MVZ 140033, MVZ 181525, MVZ 136245, MVZ 140037, MVZ 89506, MVZ 123593, MVZ 14009, MVZ 140011, MVZ 140014, MVZ 140014, MVZ 140017, MVZ 140022, MVZ 140025, MVZ 140030	
		<i>Catagonus</i>	<i>wagneri</i>	1	MVZ 145349
		<i>Pecari</i>	<i>tajacu</i>	2	MVZ 23894, MVZ 23895
	Tragulidae	<i>Tayassu</i>	<i>pecari</i>	4	NMNH 263527, NMNH 244894, NMNH 108276, NMNH 336226
		<i>Tragulus</i>	<i>kanchil</i>	3	NMNH 144151, NMNH 112009, NMNH 104428
Total			48		
GRAND TOTAL			192		

* N is specimen sample size, MVZ is Museum of Vertebrate Zoology, NMNH is National Museum of Natural History. An asterisk denotes a species with alternate genus-level classification

Almost all anthropoid primates erupt the third molar after the premolars, while the majority of strepsirrhines erupt one of the premolars after the third molar. In artiodactyls, almost all ruminants erupt the fourth premolar after the third molar, while the more basal artiodactyls (suiformes, camelids and hippopotamids) erupt the third molar after the fourth premolar. There are exceptions to the dominant dental eruption sequence in both clades. In primates, several colobine species exhibit a seemingly derived dental eruption sequence among catarrhines, where one of the premolars erupts after the third molar, or where there is variation in dental eruption sequence. *Aotus* and *Pithecia*, both New World monkeys, exhibit a dental eruption sequence different from the vast majority of anthropoids where the third molar erupts before all of the premolars are erupted. Three other New World monkeys and a colobine exhibit intraspecific variation in dental eruption sequence. Among the strepsirrhines, one lemur and two indriid species erupt the third molar after the premolars, a deviation from all other strepsirrhines sampled here.

Among artiodactyls, several caprine species erupt the third molar after the fourth premolar, a dental eruption sequence that is extremely rare among ruminants. Three other bovids, one a caprine, also exhibit near simultaneous eruption of the third molar and fourth premolar, and equally rare dental eruption sequence. Overall, there are fewer artiodactyl species than primate species that deviate from the dominant dental eruption sequence of their clade.

CHAPTER 4: Phylogeny, life history, and body size

4.1 Overview

The distribution of dental eruption sequences across primates and artiodactyls described in Chapter 3 supports a conserved phylogenetic signal for this trait. Both of my null hypotheses from Chapter 1 are tested here:

- H1₀) Dental eruption sequence is not significantly associated with life history.
- H2₀) Dental eruption sequence does not have a phylogenetic signal.

I test these hypotheses using phylogenetic independent contrasts, an analytical method that tests for correlations between traits across a phylogeny, and the D-statistic and Blomberg's K, both tests of phylogenetic signal. The methods for each of the analytical tests are described below, and the data sets used were described in detail in Chapter 3. In the next chapter (Chapter 5), I present ancestral state reconstructions of dental eruption sequence for both taxa, with fossils incorporated into the analysis in Chapter 6.

4.2 Methods of generating phylogenies

I generated phylogenies of the primate and artiodactyl samples using molecular data from the 10kTrees database (Arnold et al. 2010). Six autosomal genes, and 11 and 14 mitochondrial genes, for primates and artiodactyls respectively, were used to generate the phylogenies. In order to visualize the distribution of dental eruption sequences, I generated a phylogeny for primates (Figure 5) and artiodactyls (Figure 6) that includes all species for which I have data. Some of the species included in my study are not available in the 10kTrees database. For these, I added them manually in the Mesquite Program v. 3.11 (Maddison and Maddison 2015). *Tarsius spectrum*, *Presbytis frontata*, and *Presbytis hosei* were manually placed in the primate phylogeny using data from published literature (Shekelle et al. 2010, Vun et al. 2011). *Cebus apella + libidinosus* was placed sister to *C. apella* in the phylogeny because it is a hybrid species of *C. apella* and *C. libidinosus*. The *Ateles* phylogeny is debated (e.g., Morales-Jimenez et al. 2015), but all *Ateles* have the same dental eruption sequence in this study, so the exact distribution of species doesn't affect the ASR, and *Ateles ater* was placed sister to *Ateles belzebuth*. For artiodactyls, the manually added species are *Mazama temama*, *Muntiacus muntjac*, *Muntiacus reevesi*, *Naemorhedus milneedwardsii*, *Neotragus pygmaeus*, *Pudu mephistophiles*, *Mazama rufina*, *Rusa timorensis*, *Rucervus eldii*, *Neotragus moschatus* (Gilbert et al. 2006, Bärmann and Schikora 2014, Shi et al. 2016)

For the phylogenies, I color-coded the species names based on the distribution of dental eruption sequences across the extant tips. Blue represents a dental eruption sequence where the third molar erupts before one or more of the premolars, black represents a dental eruption sequence where the third molar erupts after the premolars, and yellow represents intraspecific variation in dental eruption sequence in primates, and simultaneous eruption of the fourth premolar and third molar in artiodactyls.

4.3 Life history and body size variables

I collected life history and body size data for the majority of primates and artiodactyls included in this study. Averages and ranges for each trait were collected from published literature, with the exception of average maximum lifespan. Values for average maximum lifespan were collected from AnAge, part of the Human Ageing Genomic Resources database (primates and artiodactyls, Tacutu et al. 2013), as well as from the Max Planck Institute of Demographic Research (primates, Carey and Judge 2000). All values, with the exception of litter size, were log corrected for the analyses.

The full list of life history and body size traits collected for primates include: maximum lifespan, average body mass of females (kilograms), average age at weaning (months), average gestation length (days), litter size, average age at sexual maturity (females, years), average body length (centimeters), age at eruption of mandibular M_1 (years), average brain mass (grams), average estrous cycle (days), and average interbirth interval (months; Table 24-25).

For artiodactyls, the full list of life history and body size traits collected include: average maximum lifespan (years), average height (centimeters), average body length (centimeters), adult body mass (kilograms), and litter size. Body mass values were taken from the average for the male of the species, but length and height values were not specified by sex (Table 26-27). Raw data and references for life history and body size variables are available for primates in Appendix C, and in Appendix D for artiodactyls.

Table 24 Descriptive statistics for life history and body size variables for primate species in which the premolars erupt last*

Life history/body size trait	PM erupt after M3			
	N	Mean	Median	Range
Maximum lifespan (yr)	12	25.5	25.4	25.0
Body mass (F, kg)	12	2.1	1.3	10.9
Age at weaning (mos)	12	5.2	4.6	8.4
Gestation length (days)	12	155.8	153.3	97.8
Litter size	12	1.2	1.0	1.0
Age at sexual maturity (F, yr)	12	1.9	1.6	2.7
Body length (cm)	11	38.0	34.8	47.3
Age at M ₁ eruption (yr)	5	0.3	0.36	0.43

* PM is premolars, M3 is third molar, N is species sample size, yr is years, F is female, kg is kilogram, mos is months, cm is centimeters, M₁ is mandibular first molar. Raw data for life history and body size traits are available in Appendix C

Table 25 Descriptive statistics for life history and body size variables for primate species in which the molars erupt last*

Life history/body size trait	M3 erupts after PM			
	N	Mean	Median	Range
Maximum lifespan (yr)	43	38.8	37.0	115.5
Body mass (F, kg)	46	9.8	6.1	74.5
Age at weaning (mos)	37	15.5	12.5	45.8
Gestation length (days)	43	190.0	180.0	144.5
Litter size	46	1.0	1.0	0.5
Age at sexual maturity (F, yr)	36	5.2	4.1	11.4
Body length (cm)	27	59.0	54.5	133.3
Age at M ₁ eruption (yr)	14	1.9	1.5	6.25

* M3 is third molar, PM is premolars, N is species sample size, yr is years, F is female, kg is kilogram, mos is months, cm is centimeters, M₁ is mandibular first molar. Raw data for life history and body size traits are available in Appendix C

Table 26 Descriptive statistics for life history and body size variables for artiodactyl species in which the fourth premolar erupts last*

Life history/body size trait	N	P4 erupts after M3		
		Mean	Median	Range
Maximum lifespan (yr)	40	21.5	21.9	25.6
Height (cm)	41	86.8	84.0	160.0
Body length (cm)	41	146.4	140.0	232.5
Body mass (kg)	43	153.0	50.0	948.0
Litter size	43	1.0	1.0	1.0

* P4 is fourth premolar, M3 is third molar, N is species sample size, yr is years, cm is centimeters, kg is kilograms. Raw data for life history and body size traits are available in Appendix D

Table 27 Descriptive statistics for life history and body size variables for artiodactyl species in which the third molar erupts last*

Life history/body size trait	N	M3 erupts after P4		
		Mean	Median	Range
Maximum lifespan (yr)	14	26.1	22.4	43.9
Height (cm)	11	91.1	82.5	82.5
Body length (cm)	9	168.4	171.0	176.5
Body mass (kg)	16	197.2	83.3	1777.0
Litter size	16	1.9	1.3	4.0

* M3 is third molar, P4 is fourth premolar, N is species sample size, yr is years, cm is centimeters, kg is kilograms. Raw data for life history and body size traits are available in Appendix D

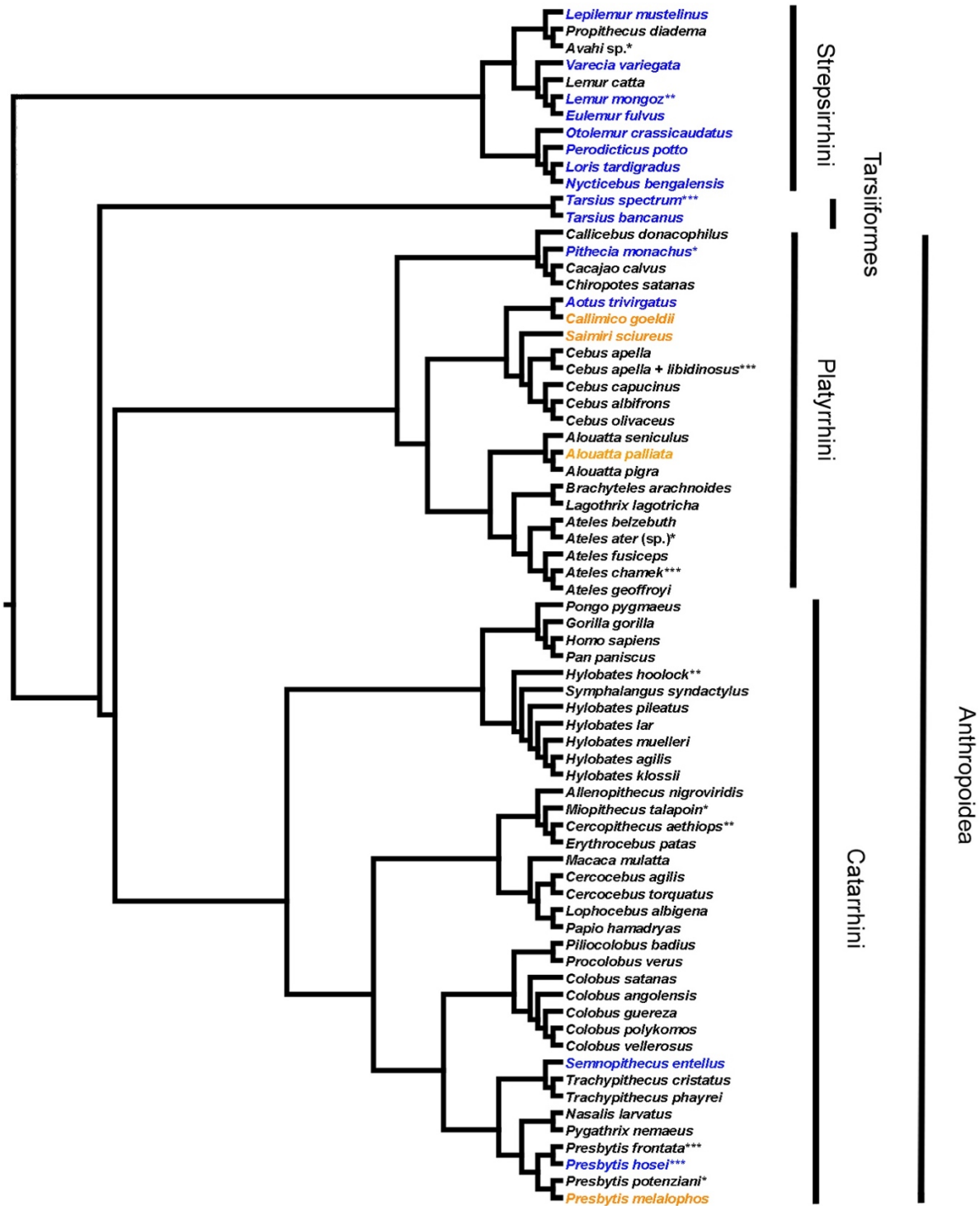


Figure 5 Phylogeny of all primate species for which dental eruption sequence is reported in this study. Black indicates that the third molar erupts after the premolars. Blue indicates that the third molar erupts before one or more of the premolars. Yellow indicates that there is intraspecific variation in the sequence of postcanine eruption. An asterisk indicates taxa for which congener molecular data from another species in the genus were used. A double asterisk indicates species with an alternate genus-level classification. A triple asterisk denotes taxa that were manually added into the phylogeny. See Chapter 4 for methods on building the phylogeny

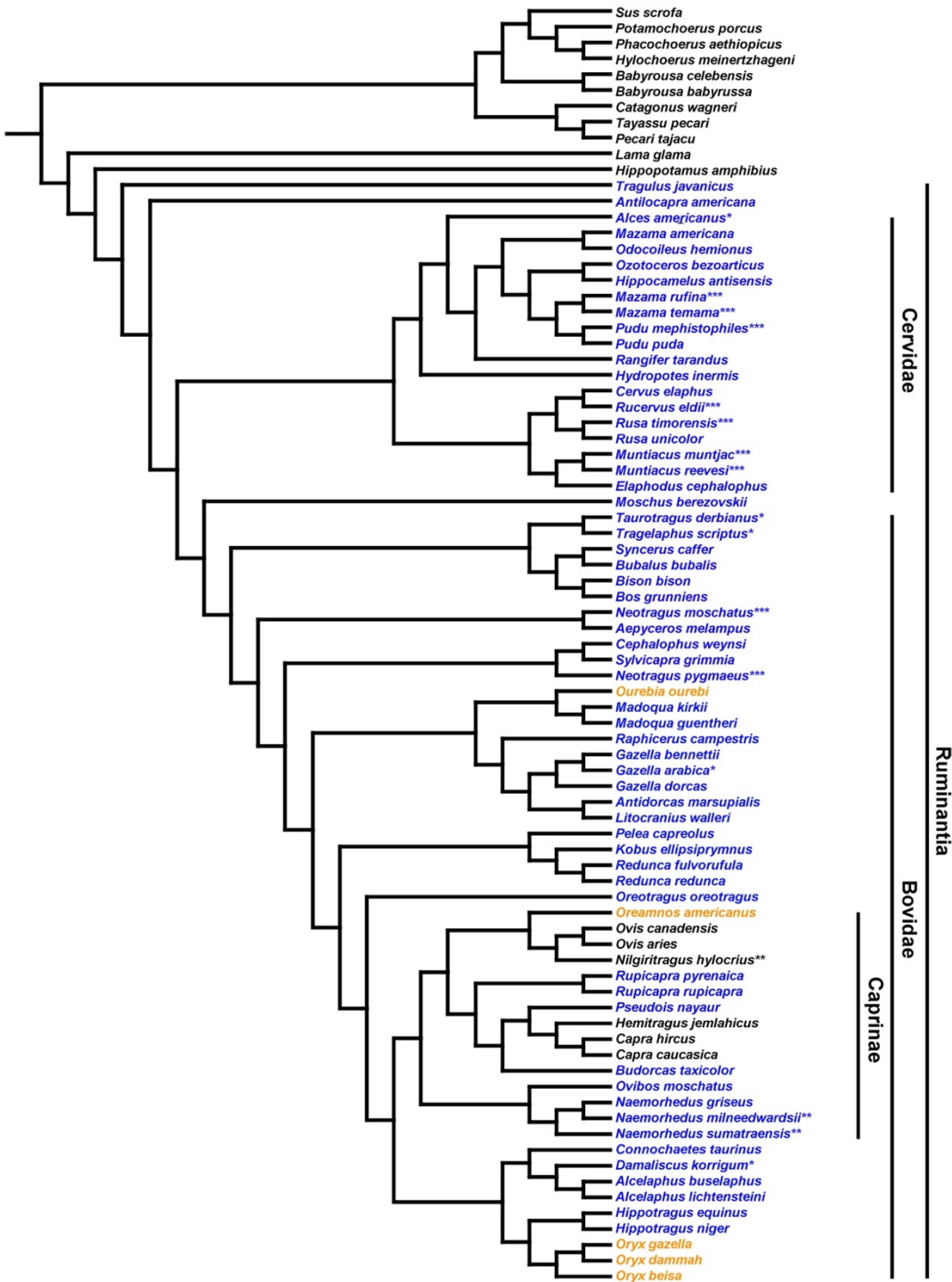


Figure 6 Phylogeny of all artiodactyl species for which dental eruption sequence is reported in this study. Black indicates that the third molar erupts after the fourth premolar. Blue indicates that the third molar erupts before the fourth premolar. Yellow indicates that third molar and fourth premolar erupt simultaneously. An asterisk indicates taxa for which congener molecular data from another species in the genus were used. A double asterisk indicates species with an alternate genus-level classification. A triple asterisk denotes taxa that were manually added into the phylogeny. See Chapter 4 for methods on building the phylogeny

4.4 Phylogenetic independent contrasts between dental eruption sequence, life history, and body size

I calculated phylogenetic independent contrasts across the 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 phylogenetic relationships of the study taxa and the number of independent trait occurrences (Ricklefs and Starck 1996). I compared dental eruption sequence with a series of life history and body size traits in primates, including The traits tested for in primates include maximum lifespan, average body mass, average age at weaning, average litter size, average age at sexual maturity, average body length, and average age at mandibular M₁ eruption. Because strong sampling of the clade is required for power when testing the PICs, there were not enough data available to test average brain mass, average estrous cycle, average gestation length, or average interbirth interval in primates.

In artiodactyls, I compared dental eruption sequence with average body mass, average litter size, average height, average length, and average maximum lifespan. In part, because many of the dental eruption studies have been focused on primates (e.g. Smith 2000), a good record of age at M₁ eruption in artiodactyls has not been compiled. As such, there are not enough available data to test this trait in artiodactyls. All independent contrasts were run through 100 iterations to account for phylogenetic uncertainty.

4.5 Results of the phylogenetic independent contrasts

For this study, I collected data for eight life history and body size traits in primates, and five life history and body size traits in artiodactyls. The descriptive statistics for each life history and body size trait are presented by dental eruption sequence for primates (Tables 24-25) and artiodactyls (Tables 26-27).

Of the 21 primate species that erupt one of the premolars after the third molar in this study, I was able to collect life history and body size data for n=5 to n=12 species. I also collected data from n=14 to n=48 primate species that erupt the third molar after one or more of the premolars. Data on average age at M₁ eruption were available for the fewest primate species relative to the other life history and body size traits sampled here. In contrast, average maximum lifespan, average body mass, age at weaning, and litter size are the traits with the best coverage across the phylogeny.

In artiodactyls, the sample size was fairly similar across the five life history and body size variables sampled in this study (Tables 26-27). For species that erupt the fourth premolar after the third molar, I collected life history and body size for n=40 to n=43 artiodactyl species. I also collected life history and body size data for n=9 to n=16 artiodactyl species that have a dental eruption sequence where the third molar erupts last.

4.5.1 Results for primates

Despite the majority of the traits exhibiting significantly conserved phylogenetic signal, the only life history or body size variable that is significantly correlated with dental eruption sequence in primates is average body mass (Table 28). The phylogenetic independent contrast for average age at sexual maturity is nearing significance ($p=0.08$), but all of the other traits,

including the life history variables, are far from significant. These data support that, independent of phylogeny, body mass and dental eruption sequence are correlated.

4.5.2 Results for artiodactyls

The sample size for artiodactyl species that erupt the fourth premolar after the third molar, for which I was also able to collect life history and body size trait information, ranges from $n=40$ to $n=43$, out of the full sample of $n=45$ for which I have 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 29). These data indicate that dental eruption sequence and the life history and body size variables sampled here, including maximum lifespan, are not correlated. The low number of independent changes in dental eruption sequence across the artiodactyl phylogeny likely contributes to the lack of significance for these phylogenetically independent contrasts, as there are few instances where the traits can be compared to dental eruption sequence.

Table 28 Phylogenetic independent contrasts between dental eruption sequence and life history/body size traits in primates*

Life history/body size trait	PIC
Average maximum lifespan (yr)	0.561
Average body mass (F, kg)	0.019
Average age at weaning (mos)	0.327
Average gestation time (days)	0.673
Average litter size	0.547
Average age at sexual maturity (F, yr)	0.076
Average body length (cm)	0.753
Average age at M ₁ eruption (yr)	0.259

* Yr is years, F is female, kg is kilogram, mos is months, cm is centimeters, M₁ is mandibular first molar, PIC is phylogenetic independent contrast. The phylogenetic independent contrast is the *p*-value for a comparison between the mean of each trait and dental eruption sequence (Ricklefs and Stark 1996). PICs in bold are significant

Table 29 Phylogenetic independent contrasts between dental eruption sequence and life history/body size traits in artiodactyls*

Life history/body size trait	PIC
Average maximum lifespan (yr)	0.935
Average height (cm)	0.528
Average length (cm)	0.261
Average body mass (kg)	0.583
Average litter size	0.929

* Yr is years, cm is centimeters, kg is kilograms, PIC is phylogenetic independent contrast. The phylogenetic independent contrast is the *p*-value for a comparison between the mean of each trait and dental eruption sequence (Ricklefs and Stark 1996). PICs in bold are significant

4.6 Tests of phylogenetic signal

In order to test for phylogenetic signal in dental eruption sequence, I 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 (Orme et al. 2015).

To test the non-binary life history and body size traits, I 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 highly phylogenetically conserved relative to Brownian motion. In contrast, $K < 1$ is generally interpreted as phylogenetically conserved, although less so than expected under a neutral conservation model. However, 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, I trimmed the trees down to only those species for which dental eruption sequence was confidently assessed (i.e., not “likely” or simultaneous), and invariable, and for which molecular data were available. In order to account for phylogenetic uncertainty, I ran both the D-statistic and Blomberg's K through 25 iterations, using 25 of the likely phylogenies generated by the 10ktrees analyses. The average of the 25 iterations was taken as the value of D and K for analysis of phylogenetic signal. All life history and body size traits, with the exception of litter size, were log corrected for analysis.

4.7 Results of the tests of phylogenetic signal

In order to test for phylogenetic signal in dental eruption sequence, life history, and body size traits, both the phylogenetic data and the variables of interest must be available for all taxa. I generated a phylogeny of the primates and artiodactyls tested in this study, the methods for which are detailed above. Dental eruption sequence, and several life history and body size traits, were tested for phylogenetic signal, and the results are discussed below.

4.7.1 Results for primates

Dental eruption sequence is phylogenetically conserved and has phylogenetic signal in primates ($D=-0.123$). This signal is not significantly different than what is expected under a neutral model of conservation ($p=0.379$), a result that is driven by the species that deviate from the dominant pattern in their clade (e.g., *Propithecus diadema*, *Semnopithecus entellus*). The majority of primate life history and body size traits analyzed here also have significant phylogenetic signals ($p < 0.05$), meaning that the distribution of each trait across the phylogeny is more conserved (i.e., changes match changes in the phylogeny) than expected under a neutral model of Brownian motion (Table 30). The traits that do not exhibit significant phylogenetic signal are average body length and average age at weaning. Of the life history and body size

traits, average age at M₁ eruption has the most conserved phylogenetic signal (K=2.29). Average body mass also has a high K-value indicating a highly conserved phylogenetic signal.

4.7.2 Results for artiodactyls

Dental eruption sequence is very phylogenetically conserved ($p=0.005$) in artiodactyls (Table 31). All of the life history and body size variables analyzed here also have a significant phylogenetic signal ($p=0.05$). Average body mass, height, length, and maximum lifespan all have K-values less than 1 indicating that these traits have a less conserved phylogenetic signal than the other traits sampled (Revell et al. 2008). Overall, 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 in artiodactyls.

Table 30 Tests of phylogenetic signal in primates*

Life history/body size trait	Blomberg's K	K <i>p</i> -value	D statistic	D <i>p</i> -value
PM erupts after M3	-	-	-0.123	0.379
Average age at M ₁ eruption (yr)	2.286	0.001	-	-
Average body mass (F, kg)	1.962	0.001	-	-
Average age at sexual maturity (F, yr)	0.849	0.001	-	-
Average gestation time (days)	0.677	0.001	-	-
Average litter size	0.514	0.009	-	-
Average body length (cm)	0.438	0.171	-	-
Average maximum lifespan (yr)	0.357	0.003	-	-
Average age at weaning (mos)	0.165	0.334	-	-

* All bolded *p*-values are significant. PM is premolars, M3 is third molar, M₁ is mandibular first molar, yr is years, F is female, kg is kilogram, cm is centimeters, mos is months. Raw data for life history and body size traits are available in Appendix C

Table 31 Tests of phylogenetic signal in artiodactyls*

Life history/body size trait	Blomberg's K	K <i>p</i> -value	D statistic	D <i>p</i> -value
P4 erupts after M3	-	-	-1.217	0.005
Average litter size	1.263	0.001	-	-
Average maximum lifespan (yr)	0.607	0.001	-	-
Average body mass (kg)	0.523	0.001	-	-
Average height (cm)	0.440	0.001	-	-
Average length (cm)	0.490	0.001	-	-

* All bolded *p*-values are significant. P4 is fourth premolar, M3 is third molar, yr is years, kg is kilogram, cm is centimeters. Raw data for life history and body size traits are available in Appendix D

4.8 Summary of the phylogenetic tests

My results demonstrate that dental eruption sequence has a conserved phylogenetic signal in primates and artiodactyls, and this signal is highly significant in artiodactyls ($p=0.005$). Most of the life history and body size traits that I examined are also phylogenetically conserved. The traits that do not exhibit phylogenetic signal are average body length in primates and average age at weaning in primates. The life history trait with the highest K-value of all traits, indicating most conserved phylogenetic signal, is average age at M₁ eruption, suggesting that this is the most phylogenetically conserved of all of the life history and body size traits sampled here. Average body mass in primates and average litter size in artiodactyls also have high K-values indicating strong phylogenetic signals.

Of all of the life history and body size traits, only body mass in primates is significantly correlated with dental eruption sequence ($p=0.019$). This correlation, tested with the phylogenetic independent contrast, takes phylogenetic relationships into account and is still significant. None of the life history or body size traits, including average body mass, are significantly correlated with dental eruption sequence in artiodactyls.

CHAPTER 5: Ancestral state reconstruction

5.1 Overview

In the previous chapter, my results show that dental eruption sequence has a conserved phylogenetic signal in primates and artiodactyls and is not correlated with life history. In this chapter, I present the results of maximum likelihood and parsimony ancestral state reconstructions using the distribution of extant dental eruption sequences reported for primates and artiodactyls in Chapter 3. In order to quantify the evolutionary context of dental eruption sequence, the most likely dental eruption sequence is described at a series of major ancestral nodes in both the primate and artiodactyl evolutionary histories. The ancestral states generated in this chapter are directly compared with what we know from the fossil record in the next chapter (Chapter 6), and the implications of these results are discussed in Chapter 7.

5.2 Ancestral state reconstruction

Also known as character mapping, ancestral state reconstruction (ASR) statistically predicts the state of each node in the phylogeny based on the distribution of a character across the tips (Felsenstein 1985, Coddington 1988, Donoghue 1989). For this reconstruction, I mapped dental eruption sequence onto the primate and artiodactyl phylogenies by creating a character state matrix. The phylogenies were constructed according to the methods detailed in Chapter 4. I ran the ancestral state reconstruction in Mesquite with Mk1 likelihood and parsimony methods (Maddison and Maddison 2015). In cases where I have phenotypic data for a species but molecular data are not available, I used congeners in the phylogeny (marked by an asterisk), or manually added the species into the phylogeny (see Chapter 4 for references for manually added species).

5.2.1 Taxonomic debates

It is important to note that debate continues about phylogenetic relationships among crown primates, as well as crown artiodactyls. In particular, the relationship of tarsiers relative to simians and strepsirrhines, has been a source of controversy (Szalay and Delson 1979, Gingerich 1981, Simons and Rasmussen 1989, Kay et al. 1997). Most recently, molecular data has been used to place tarsiers and anthropoids in a single clade, the haplorhines (Schmitz et al 2001, Jameson et al. 2011). Following the molecular data, the divergence of strepsirrhines is placed basal to tarsiers and simians in this study. The divergence of Strepsirrhini is dated to the late Mesozoic (~ 77 MA, Steiper and Young 2006), followed by the divergence of anthropoids and tarsiers approximately 65-70 MA (Pozzi et al. 2014). Within the anthropoids, the divergence of catarrhines and platyrrhines is estimated at approximately 42-50 MA, and the divergence of apes and Old World monkeys is estimated at approximately 30 MA (Steiper and Young 2006).

The relationships among crown artiodactyls are similarly controversial, and the exact timing and sequence of divergence of Suina, Camelidae, Hippopotamidae, and Ruminantia are still debated (Matthee et al. 2001, Murphy et al. 2001, Spaulding et al. 2009, Meredith et al. 2011, Zhou et al. 2011, Hassanin et al. 2012). I chose to use the phylogeny from 10ktrees, in which the divergence of Suina is placed basal to Camelidae and Hippopotamidae. Artiodactyl

species classified as “likely” erupting the fourth premolar after the third molar, or vice versa (e.g., *Axis axis*, *Moschiola meminna*), were excluded from the ancestral state reconstruction. See Chapter 3 for a complete list of dental eruption sequences.

5.3 Results of the maximum likelihood analysis in primates

Maximum likelihood analysis predicts the likelihood of a character state at each ancestral node, generating the predictions by choosing a model that maximizes the probability that the character evolved stochastically (Maddison and Maddison 2015). My ancestral state reconstruction supports that one of the premolars, rather than the third molar, erupted last in the ancestor of Primates with 97.8% likelihood (Figure 7). An even higher likelihood of 98.7% supports that the ancestor of Haplorhini erupted the third molars before one or more premolars. Following the divergence of the tarsiiiformes, the ancestral state reconstruction supports that the ancestor of simians erupted the third molar last with 87.5% likelihood. In contrast, the reconstruction supports that the ancestor of living strepsirrhines erupted the third molar before one or more premolars with 97.7% likelihood. The likelihoods of each dental eruption sequence at the major nodes are presented in Table 32.

5.3.1 Strepsirrhines

There is still some debate about the phylogenetic relationships between extant strepsirrhines (e.g., Roos et al. 2004). The distribution of dental eruption sequences across the strepsirrhine phylogeny as presented here suggests that eruption of the third molar after the premolars, as an eruption sequence, evolved twice in strepsirrhines: once in the ancestor of indriids, and again in *Lemur catta*. The ancestor of *Propithecus* and *Avahi* (Indriidae) is supported to erupt the third molar after the premolars with 90.1% likelihood. *Lemur catta* also erupts the third molar after the premolars, but the ancestor of *L. catta* and *Eulemur* is supported to have erupted the third molar before one or more of the premolars with 92.4% likelihood. There is also greater than 90% support for the hypothesis that the third molar erupted before one or more of the premolars at every other ancestral node represented within the strepsirrhine sample.

5.3.2 Tarsiiformes

Two tarsier species are represented in this sample, and they both erupt the third molar before one or more of the premolars. The ancestor of *T. spectrum* and *T. bancanus*, as well as the ancestor of tarsiers and anthropoids, is supported to erupt the third molar before the premolars with greater than 98% support. While some researchers recognize three genera of tarsiiformes (e.g., Groves and Shekelle 2010), we follow Nowak (1999) in classifying all tarsier species as belonging to *Tarsier* for this study. Further sampling of dental eruption sequences in tarsiers will reveal whether there is any interspecific variation in sequence in this group.

5.3.3 Platyrrhines

Of all the primates, platyrrhines exhibit the greatest level of variation in dental eruption sequence, as measured by the proportion of genera that deviate from the majority sequence. Both

Pithecia and *Aotus* have a dental eruption sequence like that of the strepsirrhines, where the third molar erupts before one or more of the premolars. However, the ancestor of Pitheciinae, which includes *Pithecia*, *Cacajao*, and *Chiropotes*, is supported to erupt the third molar after the premolars with 94.6% likelihood. Likewise, the ancestor of *Aotus* and the callitrichids, represented here by *Callimico*, is supported to erupt the third molar after the premolars with a 91.3% likelihood, despite the fact that neither *Aotus* or *Callimico* have that eruption sequence. The evolution of callitrichids, in general, is an interesting story (e.g., Scott 2015), and the role that dental eruption sequence plays is still unexplored. Additionally, *Saimiri* and *Alouatta* exhibit considerable variation in dental eruption sequence, but the ancestors of these genera, along with all other ancestral nodes in the phylogeny of platyrrhines, are supported to erupt the third molar after the premolars with greater than 95% likelihood.

5.3.4 Colobines

Only three cercopithecoid species, all of them colobines, have a dental eruption sequence that deviates from the primary pattern of the clade. *Semnopithecus entellus* erupts the third molar before one or more of the premolars, as does one species of *Presbytis*. Another species of *Presbytis* exhibits variation in dental eruption sequence. The ancestral state reconstruction supports that the third molar erupted after the premolars with greater than 97% likelihood at every single node in the catarrhine phylogeny which strongly suggests that these derived variations evolved relatively recently.

5.4 Results of the parsimony analysis in primates

Parsimony analysis reconstructs ancestral states using the minimum number of character changes for a given tree and acts to categorize the ancestral nodes into discrete states instead of a continuous likelihood (Maddison and Maddison 2015). Since there are three character states represented, the parsimonious likelihood of a character state can be 0%, 33.3%, 50% or 100% likely. The results of the ancestral state reconstruction using parsimony analysis are nearly identical to those using maximum likelihood analysis, translating anything above 50% likelihood as 100% parsimonious (Figure 8). The exception, and the only difference between the maximum likelihood and the parsimony results, is in reconstruction of the likelihood of dental eruption sequences at the node representing the ancestor of *Aotus* and the callitrichids, and at the node representing the ancestor of *Saimiri* and the other cebids. At these nodes, the ancestral state reconstruction under parsimony is unresolved, with equal likelihood that the third molar erupted before or after the premolars. As the New World monkey fossil record becomes more well-sampled, we will better understand the dental eruption sequence of ancestral species at these nodes.

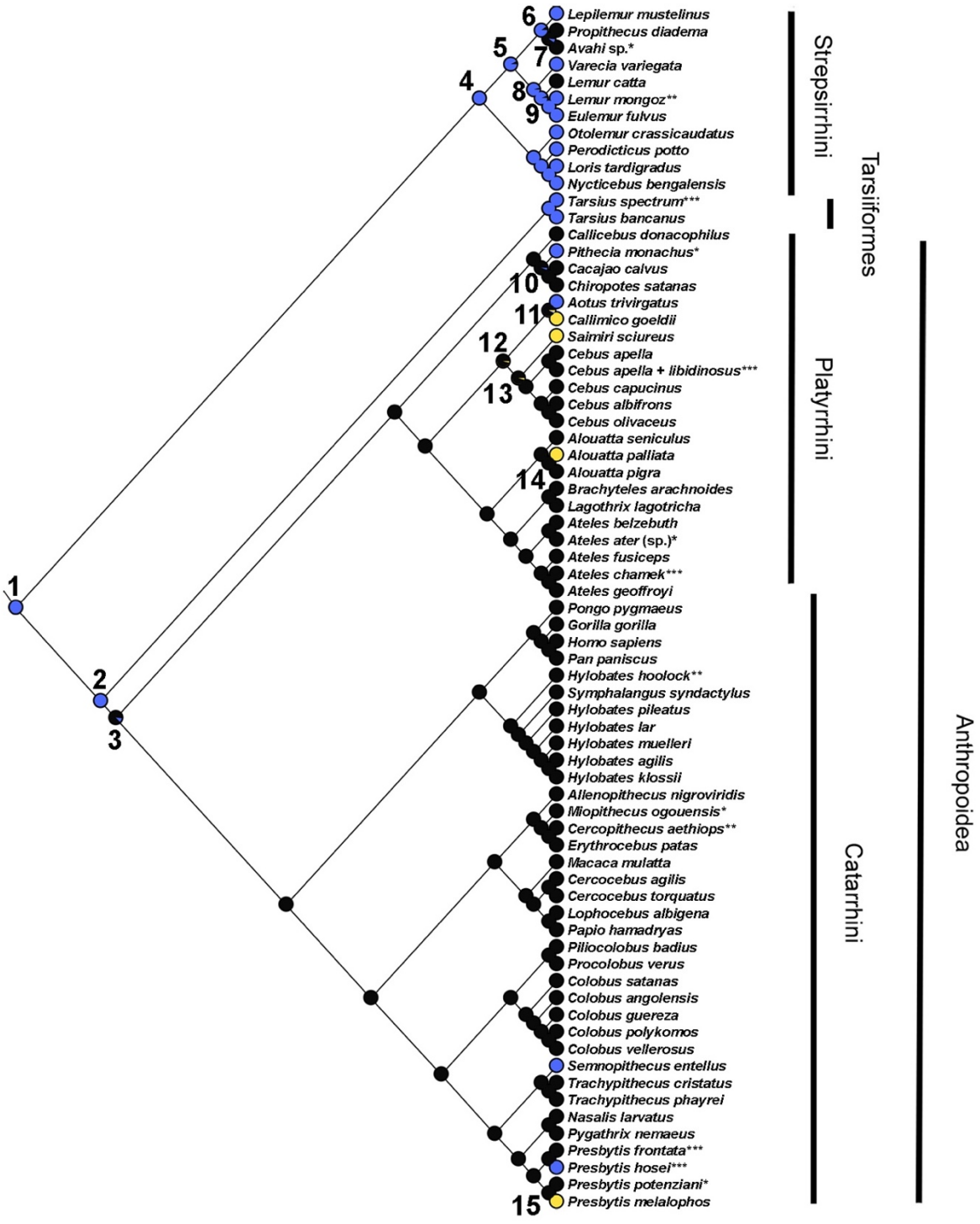


Figure 7 Results of the maximum likelihood ancestral state reconstruction in primates. Black indicates that the third molar erupts after the premolars. Blue indicates that the third molar erupts before one or more of the premolars. Yellow indicates that there is intraspecific variation in the sequence of postcanine eruption. An asterisk indicates taxa for which congener molecular data from another species in the genus were used. A double asterisk indicates species with an alternate genus-level classification. A triple asterisk denotes taxa that were manually added into the phylogeny. See Chapter 4 for methods on building the phylogeny. See Table 32 for dates at numbered nodes

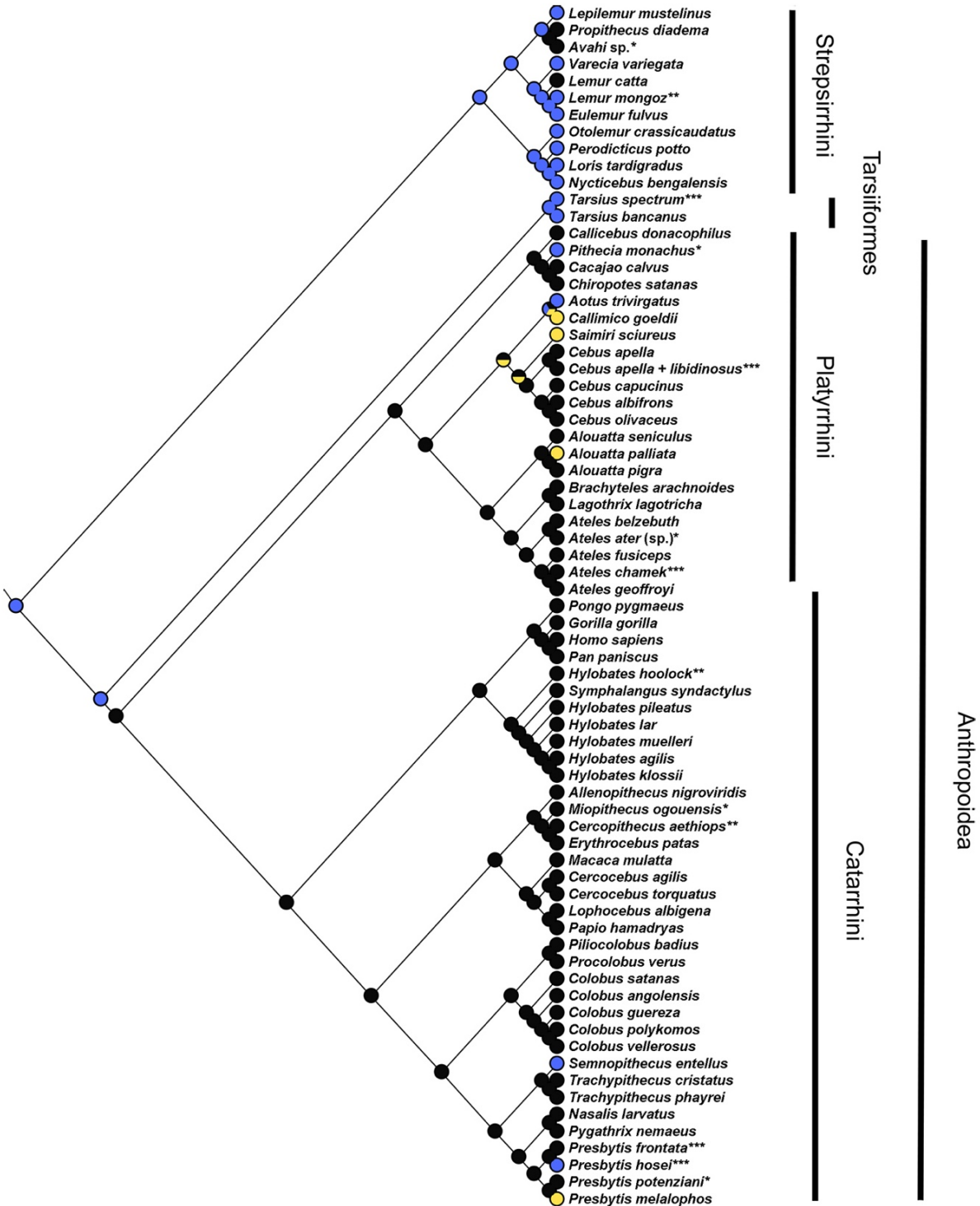


Figure 8 Results of the parsimony ancestral state reconstruction in primates. Black indicates that the third molar erupts after the premolars. Blue indicates that the third molar erupts before one or more of the premolars. Yellow indicates that there is intraspecific variation in the sequence of postcanine eruption. An asterisk indicates taxa for which congener molecular data from another species in the genus were used. A double asterisk indicates species with an alternate genus-level classification. A triple asterisk denotes taxa that were manually added into the phylogeny. See Chapter 4 for methods on building the phylogeny

Table 32 Likelihood (%) of each dental eruption sequence at each ancestral state node on the primate phylogeny*

ASR Node	Likelihood that M3 erupts after PM	Likelihood that PM erupt after M3	Likelihood of variable eruption sequence	Diverging branch	Divergence date	Reference
1	0.16%	97.80%	0.62%	Strepsirrhini	~ 77 MA	Steiper and Young 2006
2	1.19%	98.65%	0.17%	Tarsiiformes	~ 70 MA	Pozzi et al. 2014
3	87.49%	10.80%	1.72%	Platyrrhini	~ 42 MA	Steiper and Young 2006
4	1.64%	97.69%	0.67%	Lorisiformes	~ 70 MA	Yoder and Yang 2004
5	7.98%	91.36%	0.66%	Lepilemuridae + Indriidae	~ 41 MA	Yoder and Yang 2004
6	10.92%	88.18%	0.90%	Indriidae	~ 40 MA	Yoder and Yang 2004
7	90.13%	8.84%	1.03%	<i>Propithecus</i>	~ 8 MA	Perelman et al. 2011
8	5.26%	94.41%	0.33%	<i>Varecia</i>	~ 2 MA	Perelman et al. 2011
9	7.20%	92.35%	0.45%	<i>Lemur catta</i>	~ 9.7 MA	Perelman et al. 2011
10	94.58%	5.08%	0.34%	<i>Pithecia</i>	~ 13 MA	Opazo et al. 2006
11	91.30%	3.37%	5.34%	<i>Aotus</i>	~ 20 MA	Opazo et al. 2006
12	96.59%	0.71%	2.70%	Callitrichidae + Aotidae	~ 20-23 MA	Opazo et al. 2006
13	95.89%	0.68%	3.43%	<i>Saimiri</i>	~ 17 MA	Opazo et al. 2006
14	98.74%	0.02%	1.24%	<i>Allouata palliata</i>	~ 6 MA	Perelman et al. 2011
15	97.48%	0.18%	2.34%	<i>Presbytis melalophos</i>	~ 6.5-8 MA	Sturner et al. 2006

* ASR Node refers to Figure 7. M3 is third molar, PM is premolar. There are some disagreements about the exact branching order of the phylogeny

5.5 Results of the maximum likelihood analysis in artiodactyls

My ancestral state reconstruction supports that the third molar erupted last in the ancestor of Artiodactyla with 98.8% likelihood (Figure 9), and an equally high likelihood of 98.5% supports that the ancestor of artiodactyls (excepting Suina) erupted the third molar last. The likelihood of the third molar erupting last is reduced to 95.5% for the ancestor of Ruminantia + Hippotamidae. After the divergence of Hippotamidae, my ancestral state reconstruction finds support for 95.1% likelihood that the fourth premolar erupted after the third molar in the ancestor of Ruminantia. The likelihood of each dental eruption sequence at the major nodes is presented in Table 33. It is important to note that, as my 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.

5.5.1 Basal artiodactyls

All of the basal artiodactyls in this study erupt the third molar after the premolars. Support for this dental eruption sequence is greater than 99% likely at every node in the Suina clade. Because I was only able to sample a single species of camelid and a single species of hippo, and with relatively small sample sizes, I am unable to reconstruct the likelihood of the ancestors of these groups to erupt the third molar last at any nodes other than those at their divergence from more stem artiodactyls. Like their extant counterparts, there is greater than 95% support for the likelihood that the ancestors at these basal nodes erupted the third molars last.

5.5.2 Ruminants

An overwhelming majority of ruminants erupt the fourth premolar after the third molar, and there is no deviation from this sequence in any of the cervids sampled. Within the bovids, some species, primarily clustered within subfamily Caprinae, deviate from the dominant dental eruption sequence. Four non-caprines, *Ourebia ourebi* and three species of *Oryx*, exhibit simultaneous eruption of the fourth premolar and third molar. The last common ancestor of *Oryx* is supported to erupt the third molar and fourth premolar simultaneously with greater than 99% likelihood. However, the ancestor of *Oryx* and sister taxon *Hippotragus* is supported to erupt the fourth premolar after the third molar with greater than 99% likelihood. The same is true for the ancestor of *Madoqua* and *Ourebia*, again suggesting that these changes occurred relatively recently.

5.5.3 Caprines

Six caprine species have a dental eruption sequence where the third molar erupts after the premolars, and one species (*Oreamnos americanus*) exhibits simultaneous eruption of the fourth premolar and third molar. Because of uncertainty in the phylogenetic relationships of extant caprines, resolution of character states at nodes within subfamily Caprinae is subject to ambiguity. Greater sampling, as well as a more resolved phylogeny, could likely clarify the state at these nodes.

My ancestral state reconstruction supports that the ancestor of Caprinae is less than 1% likely to have erupted the third molar last. The likelihood that the third molar erupted last at the node between *Pseudois* and *Capra* is also less than 1% supported. It is not until the ancestor of *Hemitragus* and *Capra* that I find support that the third molar erupted last (> 99% likelihood). A similar pattern is found along the branch of the phylogeny leading to *Ovis*, *Nilgiritragus* (*Naemorhedus hylocrius*), and *Oreamnos*. The ancestor of this clade is supported to erupt the third molar before the fourth premolar with 78.3% likelihood. In contrast, the ancestor of *Ovis* and *Nilgiritragus* is supported to erupt the third molar after the fourth premolar with greater than 99% likelihood. Based on the distribution of dental eruption sequences across the artiodactyl phylogeny, and supported by my ancestral state reconstruction, eruption of the third molar last is either a reversal to the ancestral state, or secondarily derived, in subfamily Caprinae.

5.6 Results of the parsimony analysis in artiodactyls

Like in primates, the results of the parsimony analysis in artiodactyls are almost identical to the results of the maximum likelihood analysis. Because the parsimony analysis predicts the states at ancestral nodes as discrete categories, almost all nodes support either that the fourth premolar erupts after the third molar with 100% likelihood, or that the third molar erupts after the fourth premolar with 100% likelihood. The only exception is the node that represents the ancestor of *Oreamnos*, *Ovis*, and *Nilgiritragus*, which supports all three dental eruption sequences with equal likelihood.

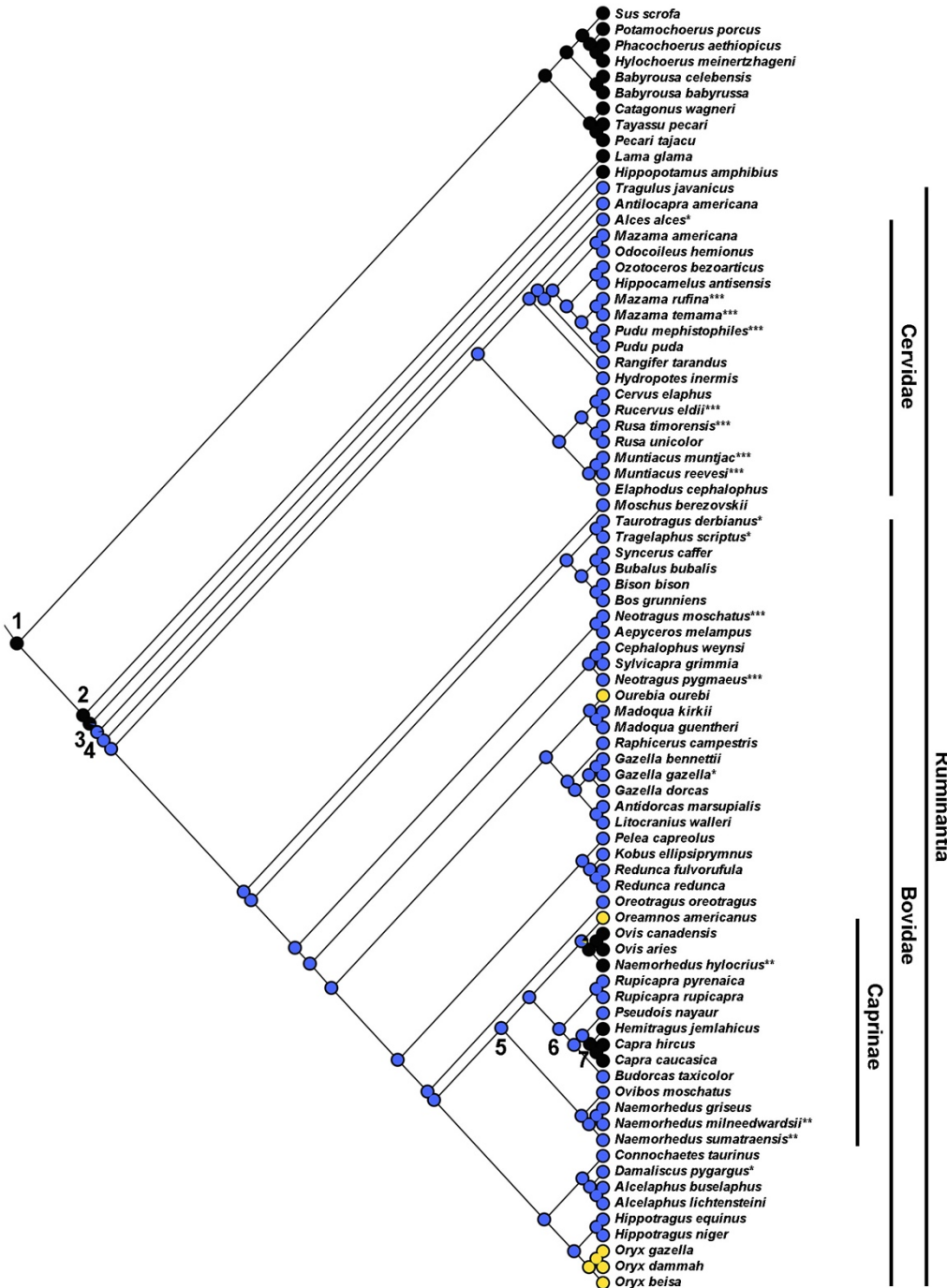


Figure 9 Results of the maximum likelihood ancestral state reconstruction in artiodactyls. Figure modified from Monson and Hlusko (2016). Black indicates that the third molar erupts after the fourth premolar. Blue indicates that the fourth premolar erupts after the third molar. Yellow indicates that the third molar and fourth premolar erupt simultaneously. An asterisk indicates taxa for which congener molecular data from another species in the genus were used. A double asterisk indicates species with an alternate genus-level classification. A triple asterisk denotes taxa that were manually added into the phylogeny. See Chapter 4 for methods on building the phylogeny. See Table 33 for dates and likelihoods at numbered nodes

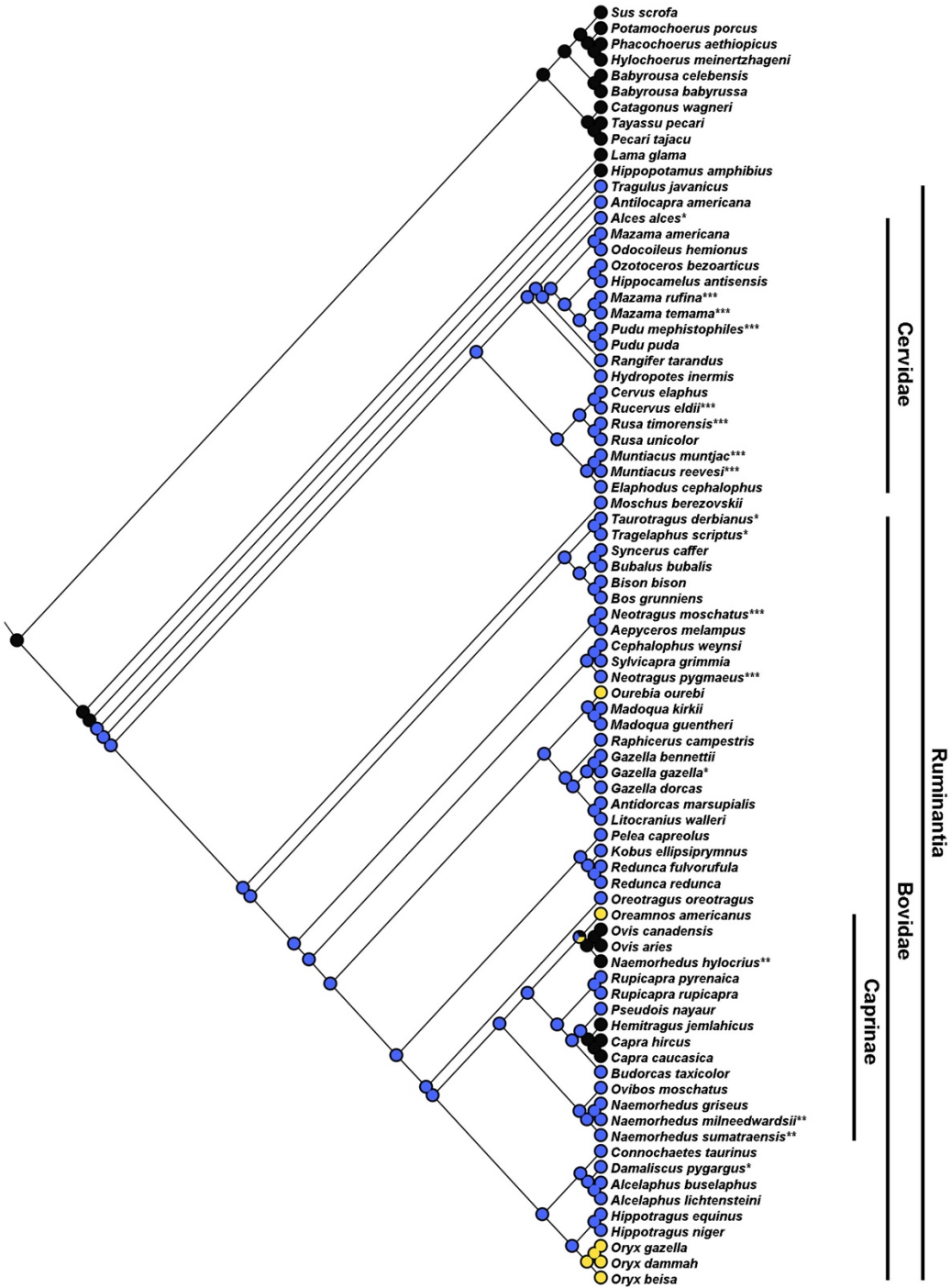


Figure 10 Results of the parsimony likelihood ancestral state reconstruction in artiodactyls. Black indicates that the third molar erupts after the fourth premolar. Blue indicates that the fourth premolar erupts after the third molar. Yellow indicates that the third molar and fourth premolar erupt simultaneously. An asterisk indicates taxa for which congener molecular data from another species in the genus were used. A double asterisk indicates species with an alternate genus-level classification. A triple asterisk denotes taxa that were manually added into the phylogeny. See Chapter 4 for methods on building the phylogeny

Table 33 Likelihood (%) of each dental eruption sequence at each ancestral state node on the artiodactyl phylogeny*

ASR Node	Likelihood that M3 erupts after P4	Likelihood that P4 erupts after M3	Likelihood of simultaneous eruption	Diverging branch	Divergence 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	Fernández and Vrba 2005
5	0.0%	100.0%	0.0%	<i>Naemorhedus</i> + <i>Ovibos</i>	~ 14.5 Ma	Fernández and Vrba 2005
6	1.3%	98.7%	0.0%	<i>Pseudois</i>	~ 11.2 Ma	Fernández and Vrba 2005
7	98.0%	1.9%	0.0%	<i>Hemitragus</i>	~ 8 Ma	Fernández and Vrba 2005

* ASR Node refers to Figure 9. M3 is third molar, P4 is fourth premolar. There are some disagreements about the exact branching order of the phylogeny. Table modified from Monson and Hlusko (2016)

My ancestral state reconstruction supports that the ancestor of primates likely erupted one or more of the premolars after the third molar. The eruption of the third molar after the premolars is an apomorphy for anthropoids within primates. I find the opposite results in artiodactyls. Ancestral state reconstruction supports that the ancestor of artiodactyls likely erupted the third molar after the premolars, and that eruption of the third molar before the fourth premolar is an apomorphy for Ruminantia within Artiodactyla. Based on the fossil record and molecular data for these groups, the anthropoid eruption sequence likely evolved in the Paleogene, approximately 45-65 MA (Beard 2002), and the ruminant eruption sequence probably evolved approximately 40-55 MA (Gentry 2000, Métais and Vislobokova 2007, Hassanin et al. 2012).

CHAPTER 6:

Incorporating the fossil record into our understanding of the evolution of dental eruption sequence in mammals

6.1 Overview

The ancestral state reconstruction performed in the previous chapter (Chapter 5) produces hypotheses about dental eruption sequences in extinct fossil taxa that may be ancestral to living taxa. In this chapter, I provide evidence for dental eruption sequences in fossil primates and artiodactyls, dated from the Paleocene to the present, and I discuss how this fossil evidence compares to the predictions of the ancestral state reconstruction. Many primate and artiodactyl fossil taxa from the Paleogene are rare and rarely preserve a full set of postcanine dentition. However, it is possible that additional examples of fossil dental eruption sequence exist in the literature beyond what is presented in this chapter. Additionally, ongoing and future paleontological excavations are likely to contribute to the fossil evidence for the evolution of dental eruption sequence in mammals.

6.2 Dental eruption sequence in fossil primates

In order to test some of the hypotheses generated by the ancestral state reconstruction (Chapter 5), I collected data on fossil specimens from collections at the University of California Museum of Paleontology in Berkeley, California, and the Ethiopian National Museum in Addis Ababa, Ethiopia (Table 34). I also gathered examples of fossil dental eruption sequences from the literature. These fossil dental eruption sequences can be directly compared to the hypothetical ancestral states predicted by the reconstruction.

6.2.1 The earliest primates

Adapids and plesiadapids are some of the earliest true primates, with fossils found throughout North America, Europe, and Asia during the Paleocene and Eocene (Gebo 2002). Fossil evidence shows that this group, although now extinct, represents a major arm of primate evolution and is extremely diverse and dispersed (Gebo 2002).

Bloch et al. (2002) present a complete dental eruption sequence for fossil plesiadapid *Acidomomys hebeticus*. This extinct species from the Paleocene of North America erupts the fourth premolar after the third molar in both the maxilla and mandible (Bloch et al. 2002). Bloch et al. (2002) cite Gingerich (1974) in arguing that the eruption sequence of *Acidomomys* is primitive, and that the derived sequence where the third molar erupts last is an adaptive response to shortening of the jaws in anthropoids, *Tarsier*, and some lemuriformes. In Smith's (2000) compilation of several dental eruption sequences from the literature for her study, she also reports that the dental eruption sequence of *Adapis parisiensis* is similar to *Acidomomys* in that the premolars erupt after the third molar (Smith 2000).

6.2.2 Early anthropoids

There is less certainty in the dental eruption sequence of early anthropoids. Kay and Simons (1983) examined 18 specimens of fossil *Parapithecus*, and 20 specimens of fossil

Apidium, both genera of parapithecids from the Oligocene of Africa, finding that *Parapithecus* is an interesting example of dental eruption sequence because the premolars and third molar appear to erupt almost simultaneously. Some researchers have hypothesized that parapithecids should be placed phylogenetically at the divergence between early anthropoids and tarsiers (e.g., Smith 1919, Kay and Simons 1983), while others include them in anthropoids (Beard 2002). At the divergence between tarsiers and stem anthropoids, my ancestral state reconstruction supports that at least one of the premolars erupted after the third molar with 64.2% likelihood. Following the divergence of tarsiers, my ancestral state reconstruction supports that the ancestor of anthropoids erupted the third molar last with 87.9% likelihood.

Based on the sequence of crown development, Conroy et al. (1975) hypothesize that *Apidium*, a fossil primate from the Oligocene, likely erupted the third molar before the premolars like other basal primates. YPM 23991, *Apidium phiomense*, shows the first and second molars in place, with the third molar missing from the open alveolus socket, and the third and fourth premolars still erupting (Conroy et al. 1975). However, more recent fossil discoveries have refuted this sequence. For example, AMNH specimen 11370, a mandible of fossil *Apidium phiomense*, is a juvenile with P₄-M₂ erupted and M₃ just beginning to erupt (Kay and Simons 1983), suggesting that the third molar may erupt after the premolar in this taxon.

Conroy et al. (1975) also suggest that YPM 23796, a fossil specimen of *Parapithecus grangeri*, erupted the third molar before one or more of the premolars based on radiographic scans of developing tooth crowns. However, subsequent fossil discoveries have shown that the third molar is the last tooth of the postcanine to erupt in extinct *P. grangeri* (Kay and Simons 1983). These specimens, generally considered to sit phylogenetically at the basal branch of Anthropoidea as sister taxa to all other anthropoids (Kay and Simons 1980, Fleagle and Kay 1987, Kay et al. 2004), or as early anthropoids (Beard 2002), are particularly interesting when considering that the vast majority of extant anthropoid species erupt the third molar after the premolars.

The dental eruption sequences of fossil *Apidium* and *Parapithecus* specimens suggest that the switch to a derived dental eruption sequence where the third molar erupts after the premolars occurred at or before the evolution of true anthropoids, likely sometime in the Paleocene or Eocene. A better understanding of the dental eruption sequence of the fossil taxa that have been more conclusively attributed to basal Anthropoidea, such as *Aegyptopithecus* and *Catopithecus* (Kay et al. 2004), is likely to contribute to further resolving the timing of this switch.

6.2.3 Cercopithecoidea

The vast majority of cercopithecoid specimens examined in this study share an anthropoid dental eruption sequence where the third molar erupts after the premolars, and my ancestral state reconstruction supports that the ancestor of cercopithecids erupted the third molar last with > 99% confidence. The dental eruption sequences of many fossil cercopithecids have been studied and published, and, to my knowledge, all of them report an anthropoid dental eruption sequence. Likewise, and in support of my ancestral state reconstruction, *Victoriapithecus*, a Miocene monkey at the base of the cercopithecoid radiation (Benefit and McCrossin 2002), erupts the third molar after the premolars (Harvati and Frost 2007).

Within the cercopithecids, all of the extant papionin genera sampled in this study (n=16) have a dental eruption sequence where the third molar erupts after the premolars. My ancestral state reconstruction supports that the ancestor of papionins also erupted the M3 last with > 99%

confidence. In order to test this hypothesis, I examined specimens at the University of California Museum of Paleontology (UCMP) in Berkeley, California. Three Plio-Pleistocene papionin fossils from South Africa are at the proper ontogenetic stage to view dental eruption sequence. Descriptions of the fossils, and their dental eruption sequences, are presented below.

UCMP 56610 is the maxilla and face of a juvenile fossil papionin, classified as extinct species *Papio izodi*. In this specimen, the majority of the adult postcanine dentition (left and right P³-M²) is fully erupted (Figure 11). The left M³ is still in the process of erupting, and a large portion of the tooth is still in the crypt of the maxilla. The right M³ has fallen out of the maxilla and is not present with the specimen. UCMP 56610 was recovered from the Buxton Limeworks (V4738) during the southern branch of the UC Africa Expedition (1947-1948) led by UCMP paleontologist Charles Camp (Monson et al. 2015).

Two other primate fossils from the southern branch of the UC Africa Expedition, stored at the UCMP, show evidence of postcanine dental eruption sequence in fossil papionins. UCMP 56660 and UCMP 125858 were both excavated from Upper Australopithecus Cave (V67275), a Plio-Pleistocene site in South Africa. UCMP 56660 is the mandible of *Parapapio antiquus*, with right P₃-M₂ fully erupted, and right M₃ in the crypt (Figure 12). The bone of the mandible surrounding the right M₃ has been removed, likely either through the excavation process, or during subsequent sampling. The left premolars are broken, but most of M₁ and M₂ are fully intact. The left M₃ is partially erupted and partially visible above the dorsal surface of the mandible.

In UCMP 125858, cf. *Papio izodi*, the mandibular postcanine is well-preserved, and the M₃ of UCMP 125858 is only partially erupted while the other molars and premolars are fully erupted and in occlusion. The left M₃ of this specimen is missing, and the right M₃ is broken on the lingual surface (Figure 13). A view of UCMP 125858 from a lateral angle (Figure 13, B) shows the broken ridge of the mandibular corpus. Although broken, it seems clear that the mandibular corpus and ramus were still covering much of the M₃ when this juvenile individual died.

Consistent with the papionins that I examined at the UCMP, more recent fossil papionin *Macaca anderssoni* (Zhoukoudian 51:8:HI, Jablonski 2002) also erupts the third molar last. Photographs of Zhoukoudian 51:8:HI, the mandible of a female *Macaca anderssoni* from the Pleistocene of China, show the M₃ clearly in the process of eruption while the permanent premolars are fully erupted in the jaw (Jablonski 2002).

The extant colobines examined in this study are much more variable in dental eruption sequence than the papionins or the apes. In spite of this, my ancestral state reconstruction supports that the ancestor of colobines erupted the third molar last with > 99% confidence, and a survey of available fossil evidence supports this reconstruction. Several fossil colobines have been reported to have the dominant anthropoid dental eruption sequence where the third molar erupts after the premolars (Harvati and Frost 2007). For example, a sample of 10 *Mesopithecus* fossils, an extinct colobine found in Europe and Asia, shows that the third molar erupts after the premolars in this taxon (Harvati and Frost 2007). Likewise, Harvati and Frost (2007) report that, like extant *Colobus*, two mandibular fossil *Colobus* specimens from Pleistocene deposits in east Africa (Kalb et al. 1982a, Harrison and Harris 1996) erupt the third molar after the premolars. Greater sampling of the fossil ancestors of *Presbytis* and *Semnopithecus* may provide insight about the recent derivation of a secondary dental eruption sequence where the third molar erupts before one or more of the premolars, or where a level of intraspecific variation in sequence is present. As these taxa evolved relatively recently and live in tropical areas of Asia, there is a

limited number of fossils in which dental eruption sequence can be observed, and no examples of dental eruption sequence in either *Presbytis* or *Semnopithecus* were noted during the literature review for this study.

6.2.4 Platyrrhines

One of the oldest known fossil platyrrhines, *Homunculus patagonicus*, conforms to the general dental eruption sequence of extant platyrrhines where the third molar erupts after the premolars (Perry et al. 2014). This dental eruption sequence is based on fossil cranial specimen MPM-PV 3505, recovered from Miocene deposits in Patagonia, Argentina (Perry et al. 2014). Although hundreds of platyrrhine fossils have been recovered, very little has been reported on dental eruption sequences in fossil platyrrhines. Greater sampling and examination of fossil platyrrhines, particularly in clades with a derived dental eruption sequence (e.g., *Aotus* and *Pithecia*), as well as those with intraspecific variation in dental eruption sequence (e.g., *Alouatta*, *Callimico*, and *Saimiri*), will clarify the evolutionary history of dental eruption sequence in these clades. It is also unclear what role the reduction of the third molars in many platyrrhines (e.g., Ford 1980) might have played in the evolution of a derived dental eruption sequence. Further study is needed to answer this question.

6.2.5 Hominoids

There has been considerable interest in understanding the dental eruption sequences of fossil hominoids (e.g., Schultz 1950, Hill 1954, Şenyürek 1955, Garn et al. 1957, Koski and Garn 1957, Dean 1985, Smith 1991, 1994, Smith et al. 1995). The relative order of emergence of the premolars compared to the second molar, in particular, has been used to differentiate fossil hominids from recent humans (e.g., Schultz 1950, Hill 1954, Şenyürek 1955). However, work by Garn et al. (1957) describes a significant level of variation in the relative eruption sequence of premolars and second molars in modern humans. They suggest that interpreting the sequence in the fossil record may be more difficult than previously thought, primarily due to the close timing of eruption of the premolars and the second molar, along with the likelihood of error in assessing eruption sequence using only bony specimens (Garn et al. 1957). While some variation in dental eruption sequence, particularly of the premolars and second molar, has been noted in other studies in humans, the eruption of the third molar after the other postcanine teeth in humans and other hominoids has not been questioned (e.g., Barrett 1957).

6.2.6 Lemuriformes

The dental eruption sequence of fossil lemuriformes has been relatively well documented (e.g., Smith 2000, Schwartz et al. 2005). According to Schwartz et al. (2005), fossil lemuriformes *Hadropithecus* and *Archaeolemur majori* erupt all of the premolars after the third molar, while multiple taxa also erupt some, but not all, of their premolars after the third molar. In contrast with *A. majori*, Schwartz et al. (2005) report that *A. edwardsi* erupts two premolars before, and one premolar after, the third molar. Fossil data also show that *Megaladapis edwardsi* erupts at least two premolars after the third molar (Schwartz et al. 2005).

Notharctus tenebrosus, a lemuriforme from the Eocene, also erupts the premolars after the third molar (Smith 2000). This fossil evidence suggests that the dental eruption sequence of

Propithecus diadema, *Avahi* sp., and *Lemur catta*, all of which erupt the third molar after the premolars, is derived in these groups. Based on the molecular data, these species have a deep evolutionary divergence dated to the Miocene (Poux and Douzery 2004, Perelman et al. 2011), after which the changes in dental eruption sequence in these taxa likely occurred.

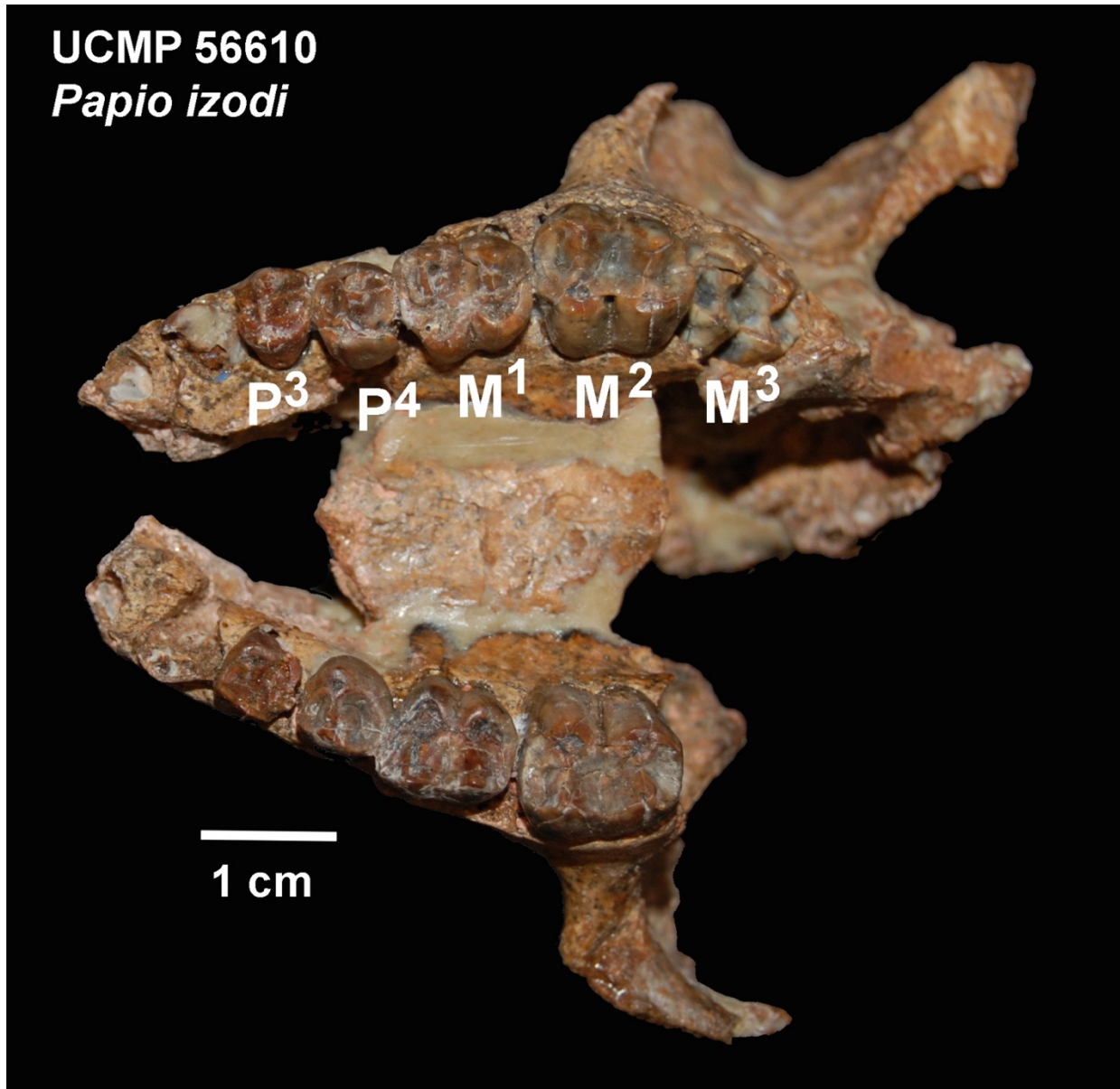


Figure 11 Example of a catarrhine dental eruption sequence in a fossil maxilla, cercopithecoid specimen UCMP 56610 (palatal view). Note the unerupted left M³

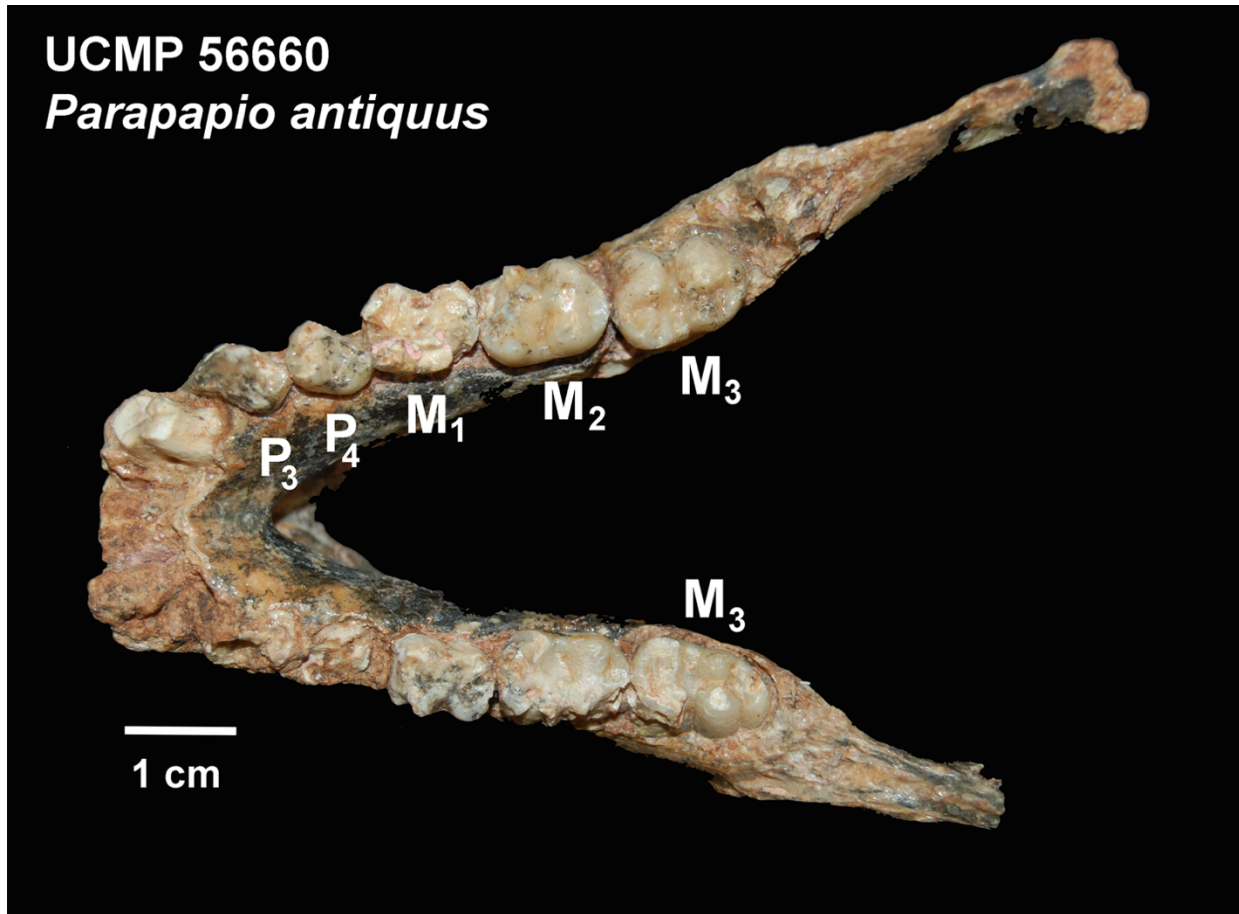


Figure 12 Example of a catarrhine dental eruption sequence in a fossil mandible, cercopithecoid specimen UCMP 56660 (occlusal view). Note the unerupted left M₃. The right M₃ has been exposed during preparation and sampling of the specimen

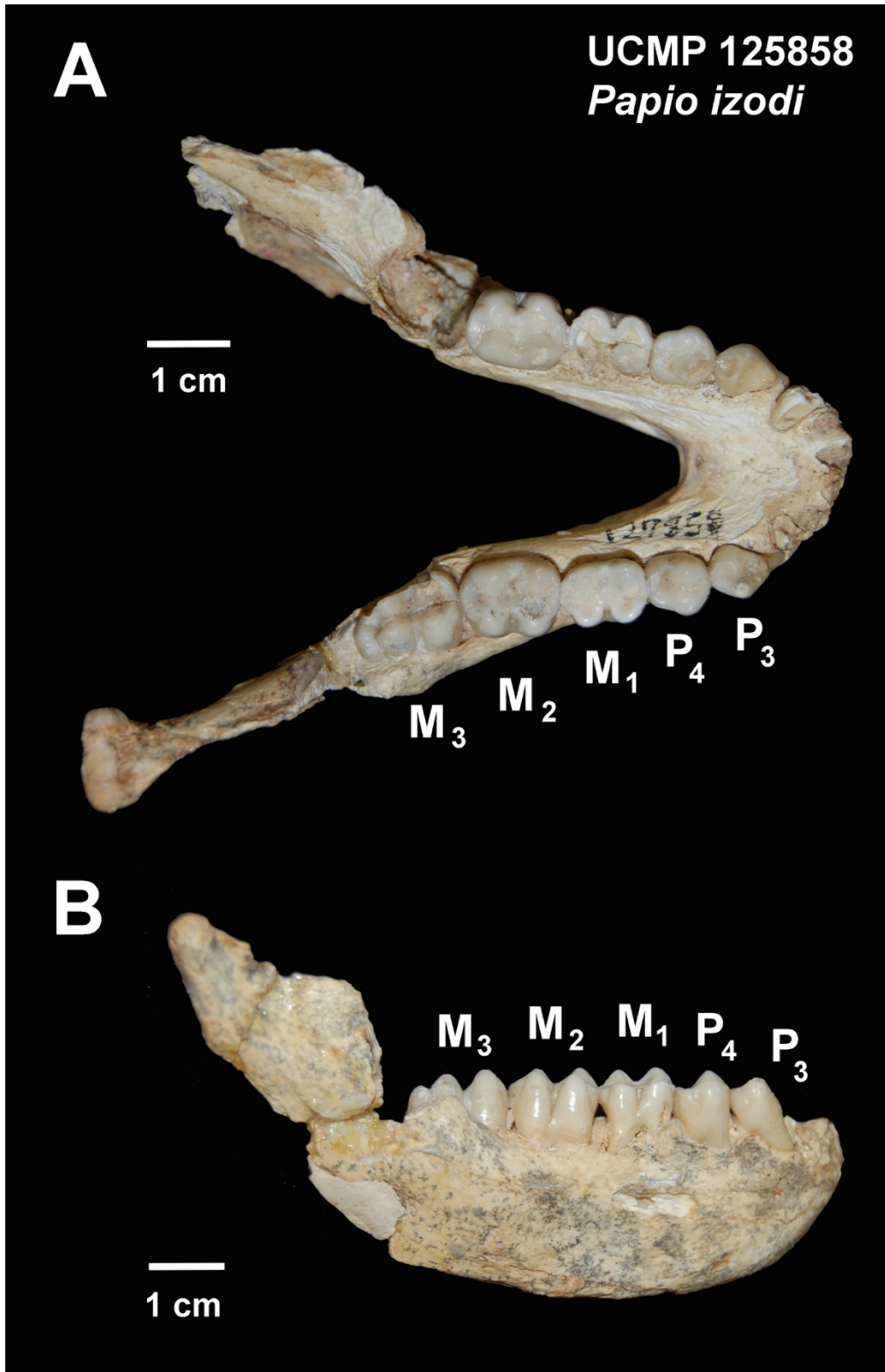


Figure 13 Example of a catarrhine dental eruption sequence in a fossil mandible, cercopithecoid specimen UCMP 125858. Note the unerupted right M₃, A) Occlusal view, B) Lateral view of the right postcanine dentition

Table 34 Fossils examined by TM for this study*

ID	Depository	Taxon	Site	Geologic age	Reference
UCMP 56610	UCMP	<i>Papio izodi</i>	Buxton Limeworks	Plio-Pleistocene	Monson et al. 2015
UCMP 56660	UCMP	<i>Parapapio antiquus</i>	Upper Australopithecus Cave	Plio-Pleistocene	Monson et al. 2015
UCMP 125858	UCMP	cf. <i>Papio izodi</i>	Upper Australopithecus Cave	Plio-Pleistocene	Monson et al. 2015
MAK VP 1/88	ENM	Suidae	Maka, Middle Awash	Pliocene	White et al. 2000
KOB VP 2/75	ENM	Suidae	Koba-ah, Middle Awash	Plio-Pleistocene	Kalb et al. 1982b
MAT 4/254	ENM	<i>Kolpochoerus</i> sp.	Matabaïetu, Middle Awash	Plio-Pleistocene	Vrba 1997
BOU-VP-1/30	ENM	<i>Sivatherium</i> cf. <i>marusium</i>	Daka, Bouri, Middle Awash	Pleistocene	Gilbert 2003
L 279-2	ENM	Hippopotamidae	Hadar	Pliocene	Geraads et al. 2012
AL 906-1	ENM	Hippopotamidae	Hadar	Pliocene	Kimbel et al. 1994

* UCMP is University of California Museum of Paleontology, ENM is Ethiopian National Museum. All UCMP specimens listed here are primate fossils from South Africa. All ENM specimens listed here are artiodactyl fossils from Ethiopia

6.3 Dental eruption sequence in fossil artiodactyls

Artiodactyls have a robust fossil record with collections excavated and held around the world (see Prothero and Foss 2007). Many of these fossil specimens retain the complete postcanine dentition. I present here the dental eruption sequences of a sample of fossil artiodactyls, with data taken both from the literature and from visual examination of specimens at the Ethiopian National Museum in Addis Ababa, Ethiopia (Table 34). The specimens described below in no way comprise the majority of fossil artiodactyl specimens with preserved dental eruption sequence, as artiodactyls are extremely well sampled in the fossil record (Prothero and Foss 2007). My goal here was to sample broadly across the families of artiodactyls, including families that persist as extant taxa as well as extinct taxa.

6.3.1 Suina

The ancestral state reconstruction in this study supports that the ancestor of extant Suina erupted the third molar after the fourth premolar with > 99% likelihood, a hypothesis that is well supported by fossil evidence. One example is fossil suid specimen KNM-SH 38051 (*Nyanzachoerus*), a right mandible with P₄-M₃, which clearly shows the fourth premolar erupted and in occlusion while the third molar is in the process of erupting (Tsujikawa 2005). This Miocene fossil from the Namurungule Formation in Kenya provides evidence that suiformes have been erupting the third molar after the premolars for at least ten million years, and likely since their purported divergence with the ancestral artiodactyl group in the Eocene (Kumar and Hedges 1998).

Three suid fossils from the Ethiopian National Museum also support the results of the ancestral state reconstruction (Table 34). MAK VP 1/88 is a fossil suid mandible with the M₃ erupting while P₃ and P₄ are fully occluded. Another fossil suid, KOB VP 2/75, is a right mandible with P₄-M₂ in occlusion and M₃ just beginning to erupt. Finally, the maxilla of a fossil *Kolpochoerus*, MAT 4/254, with M₃ erupting and P₃-M₂ in occlusion, is consistent with the other fossil specimens. Further examination of fossil suiformes, particularly fossil tayassuids, will likely provide additional support for the persistence of this trait throughout the evolutionary history of the suiformes.

6.3.2 Giraffidae

While I was 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, Table 34) gives at least one example of dental eruption sequence in this group. BOU-VP-1/30 is a right maxilla with P²-P⁴ in the crypts and visible through wear in the body of the mandible, dP³-dP⁴ in place, and M¹-M³ fully erupted. This fossil provides some limited evidence that Giraffidae, like other ruminants, likely erupts the fourth premolar after the third molar. This fossil evidence also supports my ancestral state reconstruction, which supports that the fourth premolar erupted after the third molar with greater than 99% likelihood at almost all nodes in the artiodactyl phylogeny within Ruminantia, including the node at the divergence of Giraffidae.

6.3.3 Hippopotamidae

There has been some suggestion that hippos have a more variable dental eruption sequence than was seen in this study (comment from anonymous reviewer for *Evolution*). I was able to examine 47 *Hippopotamus* and 15 *Hexaprotodon* specimens at the Museum of Vertebrate Zoology in Berkeley, California, and at the National Museum of Natural History in Washington, D.C. From these 62 specimens, only two were at the ontogenetic stage necessary to determine eruption sequence. In these two specimens (MVZ 124269 and MVZ 117895), the premolars and first two molars are fully erupted, while the third molar is only partially erupted. These two specimens support a dental eruption sequence for Hippopotamidae where the M3 erupts after the premolars, but it is possible that greater sampling of extant hippopotamids will reveal greater intraspecific variation in dental eruption sequence than was seen in this study.

I also examined several fossil hippos at the Ethiopian National Museum in Addis Ababa (Table 34), and several of these fossils suggest a level of variation in dental eruption sequence of the P4 relative to the M3 that I did not observe in my examination of extant samples. L 279-2 is a fossil maxilla with M¹-M³ fully erupted and dP⁴ sitting over the mostly, but not completely, erupted P⁴. Additionally, AL 906-1 is a maxilla exhibiting simultaneous eruption of the M³ and P⁴ on the left side of the maxilla, but not on the right. In this specimen, the P⁴ is erupting on the left side, as is the M³, but the dP⁴ is still present and in occlusion on the right side of the maxilla.

Overall, because my test of intraspecific variation was conducted extensively in ruminants and not in more basal artiodactyls, it is possible that there is greater variation in these groups. Additionally, a generally low sample size for species in Hippopotamidae, Giraffidae, and Camelidae may contribute to the lack of variation seen in this study. More extensive examination of these groups may be necessary to definitively conclude that there is no variation in dental eruption sequence in these taxa.

6.3.4 *Diplobune* †

Dental eruption sequence has been described in several extinct artiodactyl genera. Based on fossil evidence, *Diplobune*, a European artiodactyl that lived approximately 35 MA, erupted the fourth premolars after the third molar (Sudre 1974, Blondel 2001, Erfurt and Métais 2007). The date attributed to this fossil taxon, and thereby this dental eruption sequence, directly accords with my ancestral state reconstruction detailing the evolution of this phenotype approximately 40-55 MA, suggesting that either this trait is homoplastic or that *Diplobune* may have been a ruminant. Whether or not *Diplobune* should be considered a member of Ruminantia is not yet resolved (e.g., Blondel 2001, Orliac et al. 2016). Several morphological characters of *Diplobune* have generated discussion about their oddity within artiodactyls (e.g., Theodor et al. 2007) including the presence of a third toe, which has been hypothesized to be evidence of a partially, or completely, arboreal locomotor habitus (Sudre 1983, Hooker 2007, Hiard et al. 2014).

6.3.5 Caprinae

Fossil evidence from subfamily Caprinae aligns with the results of my examination of extant taxa. However, my ancestral state reconstruction supports that the fourth premolar erupts after the third molar with > 99% likelihood at the base of the tribe. At the divergence of

Pseudois, the ancestral state reconstruction supports that the fourth premolar erupts after the third molar with 98.7% likelihood, but this shifts to support that the third molar erupts after the fourth premolar with 98% likelihood. It is not until the divergence of *Capra* and *Hemitragus* approximately 8 MA (Fernández and Vrba 2005) that the ancestral state reconstruction supports that the third molar erupts after the fourth premolar as is seen in extant *Capra* and *Hemitragus*.

Myotragus, a small fossil goat endemic to the Balearic Islands of Spain, erupts the third molars after the fourth premolar 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). Jordana and Köhler (2011) used radiographic analysis of five fossil mandibles of *Myotragus balearicus* to assess dental eruption sequence in this taxon. They found that, like other caprines, *M. balearicus* erupts the third molar after the fourth premolar (Jordana and Köhler 2011). Combining this analysis of dental eruption sequence with a histological assessment of enamel microstructure, Jordana and Köhler (2011) compared tooth growth rates and crown formation time in fossil *M. balearicus* with extant caprines *Ovis* and *Rupicapra*. Jordana and Köhler (2011) estimate that the development and eruption of the postcanine dentition of *Myotragus* takes longer and is significantly later than in extant taxa. Earlier work by Köhler and Moyà-Solà (2009) examined rates of bone growth in *Myotragus* using histological analysis of fossil postcranial elements, finding that *Myotragus* grew more like crocodiles than extant mammals with what they characterize as a “slow and flexible rate” (Köhler and Moya-Sola 2009:20354). Together, these estimations provide solid evidence for the slow growth and life history of *Myotragus* (Köhler and Moyà-Solà 2009, Jordana and Köhler 2011).

Along with a slow growth rate, *Myotragus* is a dwarfed caprine, undergoing significant reduction in body size in the late Miocene after arrival on the Balearic Islands (Bate 1909, Bover and Alcover 1999, Köhler and Moyà-Solà 2009, Jordana and Köhler 2011). Some researchers have hypothesized that the slow life history of *Myotragus* is directly related to the processes driving dwarfism in this extinct genus (Köhler and Moyà-Solà 2009, Jordana and Köhler 2011). Another hypothesis that has been advanced is that limited resources on the Balearic Islands directly impacted body size, and subsequently, the development and eruption of the permanent dentition (Jordana and Köhler 2011). Interestingly, *Myotragus* also evolved a very unique dental apomorphy of continuously growing incisors, a trait that is extremely rare outside of the rodents and lagomorphs (Bover and Alcover 1999, Hillson 2005, Köhler and Moyà-Solà 2009, Tummers and Thesleff 2009, Jordana and Köhler 2011).

6.4 Summary of fossil primate and artiodactyl dental eruption sequences

The primate and artiodactyl fossil records support the results of my ancestral state reconstructions generated from a summary of dental eruption sequences in extant specimens. Fossil evidence supports that early primates had a dental eruption sequence where the third molar erupted before one or more of the premolars. Lemuriformes have also likely been erupting the third molar before one or more of the premolars since their divergence with other primates, although several taxa have secondarily evolved the ancestral dental eruption sequence. The fossil record of the anthropoids supports that the clade has been erupting the third molar after the premolars for the entirety of its evolutionary history as is predicted by the ancestral state reconstruction presented in Chapter 5.

The fossil record of the artiodactyls also supports the results of my ancestral state reconstruction based on extant taxa, although a lack of sampling in the Eocene and Oligocene has obscured the dental eruption sequences of fossil artiodactyls from these epochs. Fossil suiformes and caprines, like their extant counterparts, erupt the third molar after the fourth premolar. Based on a few specimens from the Ethiopian National Museum, fossil Giraffidae seem to have a ruminant dental eruption sequence, and fossil Hippopotamidae may exhibit some level of intraspecific variation in dental eruption sequence. Other extinct taxa (e.g., *Diplobune*), also exhibit a ruminant dental eruption sequence. As with other aspects of this study, even greater sampling of fossil and extant taxa may further clarify the evolution of dental eruption sequence in primates and artiodactyls.

CHAPTER 7: Discussion

7.1 Overview

In the previous chapters of this dissertation, I have presented an enormous amount of data describing the distribution of dental eruption sequences across extant primates and artiodactyls (Chapter 3). I have also tested the relationship between dental eruption sequence and life history (Hypothesis 1), as well as the phylogenetic signal of dental eruption sequence and all of the life history and body size traits sampled for this study (Hypothesis 2, Chapter 4). Ancestral state reconstruction of dental eruption sequence in primates and artiodactyls generates specific hypotheses about evolutionary changes in dental eruption sequence (Chapter 5), several of which I was able to test with fossil data in the previous chapter (Chapter 6). The implications of my results are discussed in this chapter. Since the data indicate that dental eruption sequence is not correlated with life history, I present several hypotheses about the drivers of dental eruption sequence in mammals. This chapter is followed by a summary of my results, conclusions, and future directions (Chapter 8).

7.2 Hypotheses about the drivers of dental eruption sequence in mammals

The data presented in this study provide a fairly clear evolutionary statement about dental eruption sequence in primates and artiodactyls, and likely other mammals. Dental eruption sequence in primates and artiodactyls is phylogenetically conserved, evidenced both by the distribution of sequences across the phylogenies of extant taxa, as well as through the statistical testing of phylogenetic signal using the D-statistic. Based on my ancestral state reconstruction, the two clades have different ancestral dental eruption sequences. Ancestral state reconstruction supports that the premolars erupt after the third molar in the ancestor of primates, and that the third molar erupts after the premolars in the ancestor of artiodactyls. Both clades exhibit a shift in dental eruption sequence early in their evolutionary history. In primates, ancestral state reconstruction supports that dental eruption sequence changed from one where the third molar erupts before the premolars, to one where the third molar erupts after the premolars, in the ancestor of anthropoids, sometime after the divergence of the tarsiers in the Paleocene (Beard 2002). In artiodactyls, ancestral state reconstruction supports that the dental eruption sequence changed from one where the third molar erupts after the premolars to one where the third molar erupts before the premolars sometime around the divergence of Ruminantia from more basal taxa, approximately 40-55 MA (Fernández and Vrba 2005).

For both primates and artiodactyls, within the clade with a derived dental eruption sequence there are several taxa that are exceptional in having a dental eruption sequence that is consistent with the ancestral condition, likely secondarily derived. Based on the morphology of these clades, and the results of the phylogenetic independent contrasts tested in this study, I have several hypotheses about the likely drivers of dental eruption sequence in these clades. In this chapter, I address each of these hypotheses as they apply to each clade individually, and to both clades more generally.

7.2.1 Body size

Dental eruption sequence is conserved in primates ($D = -0.123$), but not as conserved as in artiodactyls, a difference which may partially explain why there are more primate than artiodactyl taxa with a dental eruption sequence in exception to the dominant sequence of their clade (e.g. *Semnopithecus*, *Aotus*, etc.). Many of the life history and body size traits tested in primates are also phylogenetically conserved (Table 30). Age at eruption of M_1 has the highest K-value and is significantly phylogenetically conserved, a result that supports what has been previously published on the relationship between age at eruption of M_1 and other phylogenetically conserved traits like body size (e.g., Smith 1989, 1991, Smith et al. 1994, Kelley and Smith 2003). However, when taking phylogeny and phylogenetic signal into account, the only variable that is significantly correlated with dental eruption sequence in primates is average adult body mass.

The relationship between adult body size and dental eruption sequence in primates is significant, and it is most notable when comparing body size in anthropoids with more basal primates, the strepsirrhines and tarsiers. The vast majority of strepsirrhines and tarsiers, all small-bodied primates (e.g., Nowak 1999), have a dental eruption sequence where the third molar erupts before one or more of the premolars. In contrast, most anthropoids, larger primates on average (e.g., Nowak 1999), have a dental eruption sequence where the third molar erupts after the premolars. These two groups, strepsirrhines + tarsiers, and anthropoids, are significantly different in adult body mass ($p < 0.005$), and this is likely driving the results of the phylogenetically independent contrasts. In line with strepsirrhines and tarsiers, *Aotus*, a small-bodied platyrrhine, has the ancestral primate dental eruption sequence where the third molar erupts before the premolars. Additionally, although not included in the phylogenetic analyses, multiple taxa with variable dental eruption sequence are also small-bodied platyrrhines (*Callimico* and *Saimiri*).

Presbytis and *Semnopithecus* are not particularly small primates, even when compared to other anthropoids (Nowak 1999, Appendix C). However, there is some evidence to suggest that rapid changes in body size during the evolutionary history of these genera may have impacted craniofacial morphology (e.g. Willis and Swindler 2004, Grieco et al. 2013). This is discussed in greater detail in the chapter on dental eruption sequence in extant taxa, in the section on *Presbytis* (Chapter 3.3.4.D). The effects of rapid reductions in body size, even when the species are not small-bodied relative to other primates, may have an effect on dental eruption sequence. More extensive testing of dental eruption sequence in primates, as well as other mammalian taxa, may help illuminate the factors driving the evolution of a derived dental eruption sequence in these colobines.

In contrast to my results in primates, body mass is not correlated with dental eruption sequence in artiodactyls (Table 29) and cannot explain derived dental eruption sequence in this group. When considering some of the artiodactyls with a derived dental eruption sequence, like goats (genus *Capra*) for example, many are relatively large compared to many other bovids (Grzimek 1990). However, there is some evidence that dwarfing in caprines may further affect dental eruption sequence. *Myotragus*, a dwarfed Plio-Pleistocene fossil goat, exhibits a derived dental eruption sequence like other caprines (Jordana et al. 2013). As discussed in the previous chapter (6.3.5), researchers have proposed that the eruption of the third molar is even more delayed in *Myotragus* than in extant goats, and that this developmental delay may be related to the slower life history of the genus (Schultz's Rule), likely resulting from dwarfism and/or

resource availability on the Balearic Islands (e.g., Jordana et al. 2013). Given this fossil evidence, along with what we know about the caprines, it is possible that resource availability plays an important role in the evolution of dental eruption sequence in artiodactyls. Additionally, this provides further support for the link between changes in body size and changes in dental eruption sequence.

7.2.2 Resource availability and high-elevation habitats

The early Miocene was characterized by relatively stable and warm temperatures, a period referred to as the Miocene Climatic Optimum (Böhme 2003). During this Optimum (17-15 MA), many clades of animals, including artiodactyls, radiated rapidly, exploiting new habitats created by vegetation shifts and changing climate (Janis 1989, Zachos et al. 2001, Zhou et al. 2012). Increasing aridity in response to changes in pressure systems also expanded open grasslands, savannah, and steppe plains at both high and low elevations (Janis 1989). After the Miocene, temperatures cooled in the early Pliocene, resulting in the further spread of grasslands (Strömberg 2011). The uplifting of mountain ranges like the Himalayas, the East African Rift System, and the Rockies also occurred during this time, creating new mountain habitats yet to be occupied by radiating artiodactyls (Wolfe 1985, Janis 1989). As competition among artiodactyls increased, the caprine ancestor moved into a high-elevation niche, likely expanding into this novel habitat in response to changing ecosystems.

Caprines continue to be characterized by their ability to occupy high-elevation habitats, a characteristic that is rare among artiodactyls, and they can be found on mountain tops around the world (Vrba and Schaller 2000b). Vegetation density, composition, and quality changes with altitude (Vázquez and Givnish 1998, Shaheen and Shinwar 2012). The vegetation at high elevations is less diverse than at lower ones (e.g., Tranquillini 1964), and many plants die back completely under snow (e.g., Khan et al. 2013). It is possible that resource availability in high-elevation habitats may be associated with the evolution of the unique dental eruption sequence in caprines. Ancestral changes in habitat usage may have led to changes in diet that in turn altered the chewing stroke and bite force in goats and their relatives. Eruption of the third molars later in life guarantees that grinding teeth will be available longer in the lifespan of the animal, a trait that can potentially improve overall fitness.

In addition to the caprines sampled here, there are a few other ruminants that live in high-elevation habitats, 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). Unfortunately, I was not able to sample these taxa for this dissertation, as their rarity in population size 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 and other ruminants, will allow for more thorough testing of this hypothesis.

7.2.3 Biomechanics of chewing

Evolution of the derived dental eruption sequence of Ruminantia may be related to the synapomorphic chewing complex shared by this clade. Diet, jaw morphology and/or the biomechanics of chewing may play roles in the evolution of delayed premolar eruption in the ancestor of Ruminantia. As a clade, Ruminantia are characterized by forward placement of the

masseter muscle, one of the most important chewing muscles in mammals, and an unfused mandible (e.g. Janis 1995, Hogue and Ravosa 2001). Within artiodactyls, ruminants have evolved enlarged musculature of the masseter and a transverse chewing motion that increases occlusal contact of the teeth and allows for greater control and directionality during the chewing cycle (Fraser and Rybczynski 2014). The masseter muscle, largely thought to be adaptive in herbivores for the processing of grasses and plant materials, is directly involved in chewing and has been associated with robusticity of the mandible and maxilla (see Fraser and Rybczynski 2014). Researchers have also suggested that an enlarged masseter increases force output and is biomechanically advantageous in the processing of fibrous plant materials (Fraser and Rybczynski 2014).

In a study of 13 extant and fossil ungulate taxa, Radinsky (1985) looked at craniomandibular variation, focusing on the morphologies involved in the biomechanics of chewing. Radinsky (1985) argues that reduction of the temporal fossa and the coronoid process, along with expansion of the angular process, are related to increased masseter size, along with increased musculature related to chewing, relative to more ancestral mammals. Radinsky (1985) also makes some comment about the increase in chewing musculature in ungulates, hypothesizing it may be related to adaptive changes in the biomechanics of chewing, and particularly, the control and directionality of intense vegetation processing in the ruminants.

Additionally, interproximal tooth wear at the junction between the fourth premolar and the first molar is common in Ruminantia (personal observation) and frequently results in a concave wear pattern. This wear suggests that the fourth premolar is the site of intense chewing force and strain during feeding. Eruption of the fourth premolars after the molars may have evolved as a buffer to this chewing strain, facilitating the availability of a strong chewing surface for a longer period of time before wear causes serious health problems and even death.

7.2.4 Fusion of the mandibular symphysis

Perhaps also related to the biomechanics of chewing, there seems to be a correlation between fusion of the mandibular symphysis and dental eruption sequence. Symphyseal fusion is thought to have evolved convergently multiple times in primates as an adaptation to increasing jaw muscle force and control (e.g., Tattersall 1973, 1974, Hylander et al. 1998, Ravosa 1999, Lieberman and Crompton 2000). An unfused mandibular symphysis, like that seen in extant strepsirrhines and tarsiers, is widely supported as the ancestral state in primates (e.g., Ravosa 1999). *Eosimias centennicus*, like *Catopithecus* and other basal anthropoids, has an unfused mandibular symphysis (Beard et al. 1996). This state is shared with many omomyids and adapiformes, although, some adapiformes, like *Apidium*, also evolved a fused symphysis, likely in convergence with true anthropoids. A fused mandibular symphysis, and eruption of the third molar after the premolars, are both traits seen as early as the Oligocene in genera such as *Apidium* and *Parapithecus*. *Apidium phiomense*, like extant anthropoids, has a fused mandibular symphysis (Kay and Simons 1983), as does *Silvaladapis*, a fossil adapid from the Miocene (Gingerich and Sahni 1984). Overall, the fossil record suggests that symphyseal fusion evolved early in the anthropoid lineage (Simons 1989, 1992, Rasmussen and Simons 1992, Ravosa 1999).

Strepsirrhines have unfused mandibles, like ruminants, while anthropoids have fused mandibles like more basal artiodactyls (Hylander et al. 1998, 2000, 2004, Lieberman and Crompton 2000, Williams et al. 2010). There appears to be a correlation between symphyseal

fusion and dental eruption sequence, at least in this study. Taxa with fused symphyses overwhelmingly erupt the third molars after the premolars, while taxa with unfused symphyses erupt the premolars after the third molar. Deviations from this correlation may be representative of strong evolutionary and ecological pressures resulting from changes in diet and/or body size.

When looking through the fossil record, some researchers have suggested that a higher degree of mandibular fusion is prevalent in overall larger primate taxa (Ravosa 1996). Beecher (1983) noted that the evolution of a fused mandibular symphysis in Eocene fossil primate *Notharctus* seems to occur in step with increasing body size, while *Smilodectes* maintains small body size and an unfused mandibular symphysis. Based on the results of my study, there appears to be some relationship between body size, mandibular fusion, and dental eruption sequence in primates, and perhaps artiodactyls. However, while there are some incidences of secondary derivation, or perhaps reversal, of dental eruption sequence in extant primates, there are no known cases of change from a fused mandible to an unfused mandible in these primate taxa.

7.3 Zone of variability

The zone of variability, or the developmental variability model, was originally proposed by Bever et al. (2011) to explain changes in digit loss and digit identity in theropod dinosaurs and the evolution of the avian hand. This model is intended as a conceptual framework for interpreting the relationship between developmental processes and evolutionary changes on a broad scale (Bever et al. 2011). More specifically, the zone of variability is an area of a phylogeny where phenotypes are more variable, and it directly precedes a change in phenotype (Bever et al. 2011). According to Bever et al. (2011),

“A Darwinian model of evolution predicts that transformations are punctuated by an increase in the probability that development will produce either the ancestral or derived condition. The area in time and tree space characterized by this increased probability is here termed a “zone of variability” (Bever et al. 2011:276).

While this model was developed to understand changes in digit morphology and digit number, the concept seems well-applied to switches from an ancestral to a derived phenotype as is seen in several cases in my data. Many taxa with a variable dental eruption sequence in this study are taxa that are phylogenetically close to other taxa with a derived dental eruption sequence. For example, *Oreamnos* exhibits simultaneous eruption of the fourth premolar and the third molar and is sister taxa to *Ovis*, with a derived dental eruption sequence, within the caprines. Assessment of a dental eruption sequence as simultaneous, however, could be a product of low sample size in this taxon, and dental eruption sequence in artiodactyls has a strongly significant phylogenetic signal, so there is limited evidence for a zone of variability in artiodactyls. In primates, there is more clustering of variable and derived dental eruption sequences within larger clades. In platyrrhines, *Callimico* exhibits intraspecific variation dental eruption sequence and is sister to *Aotus*, a taxon with a derived dental eruption sequence. Squirrel monkeys, *Saimiri sciureus*, also exhibit intraspecific variation in dental eruption sequence and are in family Cebidae, phylogenetically sister to *Callimico* and *Aotus*.

In colobines, one species of *Presbytis* exhibits intraspecific variation in dental eruption sequence while another has a derived sequence. *Semnopithecus*, with a derived dental eruption

sequence, is also phylogenetically close to *Presbytis* (e.g., Oppenheimer 1977, Pozzi et al. 2014). The rearrangement of species within *Presbytis* (e.g., Sterner et al. 2006) casts some doubt on the conclusiveness of intraspecific variation in this genus, but greater sampling will likely clarify patterns of dental eruption sequence in this clade. Overall, there is some evidence to suggest that the concept of a zone of variability may apply, in a limited fashion, to the distribution of dental eruption sequences across the primate and artiodactyl phylogenies. This suggests the possibility that variation in dental eruption sequence can precede expression of the derived sequence.

Chapter 8: Conclusion

8.1 Overview

In the chapters preceding this one, I have presented the methods for study of dental eruption sequence and the results of my investigation. I tested both hypotheses and found that dental eruption sequence has a conserved phylogenetic signal in mammals (Hypothesis 2) but is not correlated with life history (Hypothesis 1, null). I have also presented ancestral state reconstructions of dental eruption sequence for primates and artiodactyls (Chapter 5), and incorporated data from the fossil record (Chapter 6). Some hypotheses about the drivers of the evolution of dental eruption sequence in mammals, including possible associations with body size, mandibular fusion, and resource availability, were presented in the discussion (Chapter 6). This chapter summarizes the results of this dissertation and offers some conclusions about the applicability of Schultz's Rule to mammalian evolution. In this chapter, I also present some future directions for dental eruption sequence research, including ideas about increasing extant and fossil sample size, investigating dental eruption sequence in the anterior dentition, and sampling in other taxa. Finally, I conclude with a statement on the overall importance of this research.

8.2 Summary of results

The results of this study clearly show that dental eruption sequence is phylogenetically conserved in primates and artiodactyls, and, contrary to the hypothesis postulated by Schultz's Rule, is not correlated with life history in either of these taxa. However, average adult body mass is significantly correlated with dental eruption sequence in primates. This correlation is driven by the strepsirrhines and tarsiiiformes, as well as a few platyrrhine taxa. Several primate species also exhibit intraspecific variation in dental eruption sequence, including three platyrrhines and two colobine species.

In contrast, there is no correlation between body mass, or life history, and dental eruption sequence in artiodactyls, despite a highly significant phylogenetic signal for eruption sequence in this group. The caprines are unique among Ruminantia in erupting the third molar after the premolars, and their fossil record and extant distribution suggest that limited resource availability may be playing a role in the evolution of the derived dental eruption sequence in this group.

Overall, my results suggest that the morphology of the mandible and its affect on the biomechanics of chewing is likely a significant factor driving changes in dental eruption sequence in mammals. Mandibular symphyseal fusion is a diagnostic feature of almost all of the taxa in this study that erupt the third molars after the premolars. And changes in mandibular symphyseal fusion directly coincide with evolutionary changes in dental eruption sequence in both primates and artiodactyls. Work in primates has shown a positive relationship between body size and mandibular symphyseal fusion, further bolstering the link between dental eruption sequence and these two phenotypes.

The distribution of variation in dental eruption sequence across the primate and artiodactyl phylogenies also lends some support to the hypothesis of a zone of variability (Bever et al. 2011), where there is a tendency for taxa exhibiting intraspecific variation in dental eruption sequence to be sister to, and often basal to, taxa with a derived dental eruption

sequence. Given this association, it is possible that intraspecific variation in dental eruption sequence is a precursor step to the evolution of a derived dental eruption sequence. Additionally sampling of dental eruption sequence in mammalian taxa may provide further support for this hypothesis.

8.3 Re-evaluating Schultz's Rule

Schultz's Rule specifically states that dental eruption sequence is correlated with rates of post-natal growth and longevity. The traits most frequently used to test Schultz's Rule are age at eruption of M_1 , age at weaning, and maximum lifespan (e.g., Smith 2000, Guthrie and Frost 2011, Hellmund 2013, 2016, Jordana et al. 2013). While these three traits are phylogenetically conserved, they are not significantly associated with dental eruption sequence in primates. A superficial correlation appears when comparing the dental eruption sequences of select taxa with lifespan, age at eruption of M_1 , and age at weaning (e.g., Smith 2000, Hellmund 2013, 2016, Jordana 2013). However, when phylogeny is taken into account, a necessary correction since these traits are phylogenetically conserved, there is no correlation between dental eruption sequence and any of these traits. Any qualitative correlation observed is likely an indirect product of overlapping phylogenetic signal. In support of the original hypotheses underlying Schultz's Rule, there is a relationship between dental eruption sequence and life history. However, this relationship is entirely indirect and therefore should not be used to interpret the life histories of fossil taxa.

Based on the results of this study, dental eruption sequence in fossil primates can be used as evidence of phylogenetic affiliation, and to some degree, adult body size. However, dental eruption sequence of fossil primates should not be used as direct evidence of life history as has been the case in past studies (e.g., Schwartz et al. 2005, Robson and Wood 2008, Franzen et al. 2009). Instead, fossils can be attributed phylogenetically, and based on the relationship between life history variables and that particular phylogenetic group, some statements about life history may be made. Overall, this study highlights the need to account for the complexities of mammalian evolution, morphology, and life history when attempting to disentangle the relationships between various aspects of these characters.

8.4 Future directions

This study is the most comprehensive examination of dental eruption sequences in both primates and artiodactyls. However, there are several ways this research can be expanded to more fully test the relationship between dental eruption sequence and phylogeny, life history, and body size. Increasing sample size, incorporating more fossil data, investigating the anterior dentition, and adding in more taxa to the analyses are discussed below as ways to further expand on this research.

8.4.1 Sample size

Greater sampling will continue to resolve the relationship between dental eruption sequence and body size, as well as provide further evidence in support of, or against, the hypotheses of the ancestral state reconstructions in this study. Due to low sample sizes, in some cases I determined the dental eruption sequences of primate and artiodactyl species based on

only a few specimens. Greater sampling of these species will bear greater support for these sequences and will likely further resolve cases of intraspecific variation in dental eruption sequence.

Along with increasing sample sizes of the species discussed here, increasing the number of species with known dental eruption sequence will further resolve the relationship between eruption sequence, body size, mandibular fusion, the biomechanics of chewing, and resource availability, as well as provide further data to test whether the distribution of eruption sequences across extant taxa supports the hypothesis of a zone, or zones, of variability. Likewise, further sampling of species in clades with derived dental eruption sequences and intraspecific variation in eruption sequence will increase our understanding of this variation. In primates in particular, greater sampling of *Presbytis*, *Alouatta*, and *Semnopithecus* will contribute to our understanding of the evolution of dental eruption sequence in these distinctive groups.

8.4.2 Better resolution of the fossil record

In addition to greater sampling of extant species, increased sampling of the fossil record will further resolve our understanding of the evolution of dental eruption sequences in primates and artiodactyls. Our knowledge of the timing of changes in dental eruption sequence is tied to the fossil record and the estimated timing of divergences. Additionally, the fossil record can shed light on whether repeated instances of derived dental eruption sequences (e.g. Caprinae, *Presbytis* and *Semnopithecus*, *Aotus* and *Callimico*) are convergent and secondarily derived, or ancestral, within that clade. Increased sampling of Paleogene primates and artiodactyls, in particular, will further resolve dental eruption sequence in many of the extinct taxa, and it may contribute to phylogenetic hypotheses about relationships between these extinct groups and crown taxa.

8.4.3 The anterior dentition

This study compares the eruption sequence of the third molar relative to the premolars in primates and artiodactyls. Schultz's Rule specifically cites the eruption sequence of the replacement teeth relative to the molars (Smith 2000). I chose to restrict my study to the postcanine dentition because previous work in mice and baboons has shown the genetic and phenotypic independence of the anterior and postcanine dentition (Hlusko et al. 2011). Given the phylogenetic signal of the relative eruption sequence of the postcanine dentition, I hypothesize that the relative eruption sequence of the anterior compared to the postcanine dentition also has a phylogenetic signal, although I do not have the data here to test that hypothesis. If there is a phylogenetic signal in the relative eruption sequence of the anterior to postcanine dentition, it is possible that changes in eruption sequence may be driven by body size, or possibly mandibular symphyseal fusion, as seen in this study, or by other life history variables.

8.4.4 Sampling in other taxa

The most direct extension of this work is the investigation of dental eruption sequence in other mammalian taxa. An increase in known dental eruption sequences, along with greater incorporation of the fossil record, will also help resolve the evolution of dental eruption sequence more broadly across mammals. The dental eruption sequence of additional mammalian groups

with mandibular symphyseal fusion, like some carnivores and marsupials (Ravosa and Hogue 2004), will be particularly interesting to explore given the relationship between symphyseal fusion and dental eruption sequence seen in this study.

8.5 Importance of this study

This study is the most comprehensive collection of dental eruption sequences in primates or artiodactyls, and the evidence strongly supports that eruption sequence is phylogenetically conserved in mammals. This study also highlights the importance of teasing out the complexities of mammalian morphological evolution. Dozens of researchers have used Schultz's Rule to make assumptions about extinct and extant taxa (e.g., Macho and Williamson 2002, Loe et al. 2004, Schwartz et al. 2005, Robson and Wood 2008, Asher and Olbricht 2009, Dirks et al. 2009, Franzen et al. 2009, Townsend and Croft 2010, Yamanaka et al. 2010, Billet and Martin 2011). However, more intensive testing of Schultz's Rule with a larger, more phylogenetically diverse group of mammals, shows that any correlations between dental eruption sequence and life history are superficial. Dental eruption sequence, life history, and body size all carry a conserved phylogenetic signal. But only body size is correlated with dental eruption sequence when phylogeny is taken into account, and only in primates. My data also suggest that body size, mandibular symphyseal fusion, and the biomechanics of chewing may have intertwined influences on the evolution of dental eruption sequence.

Moving forward, I would encourage researchers to stop using Schultz's Rule to interpret the life history of extinct or extant mammals. However, dental eruption sequence is phylogenetically conserved and can therefore be used to weigh in on taxonomic debates. Once a species or specimen has been attributed to a particular taxonomic group, understanding the phylogenetic distribution of life history traits of interest within that group will allow researchers to make more precise statements characterizing extinct taxa.

One of the most important aspects of science is to build off of previous work with new samples, new methods, and new technologies. This study was inspired by countless hours examining mammalian teeth in the Museum of Vertebrate Zoology and the prominent work of Schultz (1935, 1956, 1960) and Smith (1994, 2000), which, like all good science, has given rise to many more research questions and hypotheses. My findings here revise previous studies through an increase in sampling and updated phylogenetic tests. I can only hope that the findings presented here will inspire many more research questions and hypotheses, and the testing and retesting of my hypotheses, in the future.

References

- Arnold C, Matthews LJ, Nunn CL (2010) The 10kTrees website: a new online resource for primate phylogeny. *Evolutionary Anthropology* 19:114-118
- Asher RJ, Olbricht G (2009) Dental ontogeny in *Macroscelides proboscideus* (Afrotheria) and *Erinaceus europaeus* (Lipotyphla). *Journal of Mammalian Evolution* 16(2):99-115
- Bärmann EV, Schikora T (2014) The polyphyly of *Neotragus* – results from genetic and morphometric analyses. *Mammalian Biology-Zeitschrift für Säugetierkunde* 79(4):283-286
- Barrett MJ (1957) Dental observations on Australian aborigines: tooth eruption sequence. *Australian Dental Journal* 2:217-227
- Barry JC (1987) The history and chronology of Siwalik cercopithecids. *Human Evolution* 2(1):47-58
- Bate DM (1909) I—Preliminary note on a new artiodactyl from Majorca, *Myotragus balearicus*, gen. et sp. nov. *Geological Magazine (Decade V)* 6(09):385-388
- Beard KC (1998) A new genus of tarsiidae (Mammalia: Primates) from the Middle Eocene of Shanxi Province, China, with notes on the historical biogeography of tarsiers. *Bulletin of Carnegie Museum of Natural History* 34:260-277
- Beard KC (2002) Basal anthropoids. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 133-150
- Beard KC, MacPhee RD (1994) Cranial anatomy of *Shoshonius* and the antiquity of Anthropoidea. In: Fleagle JG, Kay RF (eds) *Anthropoid Origins*. Springer, New York, pp 55-97
- Beard KC, Qi T, Dawson MR, Wang B, Li C (1994) A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature* 368(6472):604
- Beard KC, Tong Y, Dawson MR, Wang J, Huang X (1996) Earliest complete dentition of an anthropoid primate from the late middle Eocene of Shanxi Province, China. *Science* 272(5258):82
- Beecher RM (1983) Evolution of the mandibular symphysis in Notharctinae (Adapidae, Primates). *International Journal of Primatology* 4(1):99-112
- Benefit BR, McCrossin ML (2002) The Victoriapithecidae, Cercopithecoidea. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 241-254

- Bennett EL, Davies AG (1994) The ecology of Asian colobines. In: Davies AG, Oates J (eds) *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge University Press, Cambridge, pp 129-172
- Bever GS, Gauthier JA, Wagner GP (2011) Finding the frame shift: digit loss, developmental variability, and the origin of the avian hand. *Evolution and Development* 13(3):269-279
- Bibi F (2013) A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. *BMC Evolutionary Biology* 13(1):166-171
- Billet G, Martin T (2011) No evidence for an afrotherian-like delayed dental eruption in South American notoungulates. *Naturwissenschaften* 98(6):509-517
- Bloch JI, Boyer DM, Gingerich PD, Gunnell GF (2002) New primitive paromomyid from the Clarkforkian of Wyoming and dental eruption in Plesiadapiformes. *Journal of Vertebrate Paleontology* 22(2):366-379
- Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57(4):717-745
- Blondel C (2001) The Eocene–Oligocene ungulates from Western Europe and their environment. *Palaeogeography, Palaeoclimatology, Palaeoecology* 168(1):125-139
- Böhme M (2003) The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195(3):389-401
- Bover P, Alcover JA (1999) The evolution and ontogeny of the dentition of *Myotragus balearicus* Bate, 1909 (Artiodactyla, Caprinae): evidence from new fossil data. *Biological Journal of the Linnean Society* 68(3):401-428
- Bowyer R (1997) The role of moose in landscape processes: effects of biogeography, population dynamics and predation. In: Bissonette J (ed) *Wildlife and Landscape Ecology: Effects of Sequence and Scale*. Springer-Verlag, New York, pp 265-287
- Brandborg SM (1950) *The life history and ecology of the mountain goat in Idaho and Montana*. Masters of Science Dissertation, University of Idaho
- Brooks DM, Tarifa T, Rojas JM, Vargas RJ, Aranibar H (2001) A preliminary assessment of the mammalian fauna of the eastern Bolivian panhandle. *Mammalia* 65(4):509-520
- Bryant HN (1990) Implications of the dental eruption sequence in *Barbourofelis* (Carnivora, Nimravidae) for the function of upper canines and the duration of parental care in sabretoothed carnivores. *Journal of Zoology* 222(4):585-590

- Buzan EV, Bryja J, Zemanová B, Kryštufek B (2013) Population genetics of chamois in the contact zone between the Alps and the Dinaric Mountains: uncovering the role of habitat fragmentation and past management. *Conservation Genetics* 14(2):401-412
- Byrd KE (1979) *Sequences and asymmetries of dental development and eruption in the Ceboidea*. Doctoral Dissertation, University of Washington
- Byrd KE (1981) Sequences of dental ontogeny and callitrichid taxonomy. *Primates* 22(1):103-118
- Cahill DR (1969) Eruption pathway formation in the presence of experimental tooth impaction in puppies. *Anatomical Records* 164:67-77
- Cahill DR, Marks SC Jr, Wise GE, Gorski JP (1988) A review and comparison of tooth eruption systems used in experimentation - a new proposal on tooth eruption. In: Davidovitch Z (ed) *The Biological Mechanisms of Tooth Eruption and Root Resorption*. EBSCO Media, Birmingham, pp 1-7
- Carey JR, Judge DS (2000) *Monographs on Population Aging, 8*. Odense University Press, Southern Denmark
- Chaimanee Y, Lebrun R, Yamee C, Jaeger JJ (2010) A new middle Miocene tarsier from Thailand and the reconstruction of its orbital morphology using a geometric-morphometric method. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20102062
- Cifelli RL, de Muizon C (1998) Tooth eruption and replacement pattern in early marsupials. *Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science* 326(3):215-220
- Coddington JA (1988) Cladistic tests of adaptational hypotheses. *Cladistics* 4(1):3-22
- Conroy GC, Schwartz JH, Simons EL (1975) Dental eruption patterns in Parapitheciidae (Primates, Anthroidea). *Folia Primatologica* 24(4):275-281
- Cortés-Ortiz L, Bermingham E, Rico C, Rodríguez-Luna E, Sampaio I, Ruiz-García M (2003) Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. *Molecular Phylogenetics and Evolution* 26(1):64-81
- Covert HH (2002) The earliest fossil primates and the evolution of prosimians. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 13-20
- Dagosto M, Gebo DL, Beard KC, Qi T (1996) New primate postcranial remains from the middle Eocene Shanghuang fissures, southeastern China. *American Journal of Physical Anthropology* 22:92-93

- Dean MC (1985) The eruption pattern of the permanent incisors and first permanent molars in *Australopithecus (Paranthropus) robustus*. *American Journal of Physical Anthropology* 67(3):251-257
- Delpero M, Masters JC, Cervella P, Crovella S, Ardito G, Rumpler Y (2001) Phylogenetic relationships among the Malagasy lemuriforms (Primates: Strepsirrhini) as indicated by mitochondrial sequence data from the 12S rRNA gene. *Zoological Journal of the Linnean Society* 133(1):83-103
- Dirks W, Anemone RL, Holroyd PA, Reid DJ, Walton P (2009) Phylogeny, life history and the timing of molar crown formation in two archaic ungulates, *Meniscotherium* and *Phenacodus* (Mammalia, 'Condylarthra'). In: Koppe T, Meyer G, Alt K (eds) *Comparative Dental Morphology, Vol. 13*. Karger Publishers, Basel, pp 3-8
- Donoghue MJ (1989) Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. *Evolution* 43(6):1137-1156
- Erfurt J, Métais G (2007) Endemic European Paleogene artiodactyls. In: Prothero DR, Foss SE (eds) *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore, pp 59-84
- Eudey AA (1987) Action plan for Asian primate conservation. *International Union for the Conservation of Nature and Natural Resources/Species Survival Commission Primate Specialist Group, World Wildlife Fund, and the United Nations Environment Programme*, Washington, DC, pp 1-70
- Felsenstein J (1985) Phylogenies and the comparative method. *American Naturalist* 125:1-15
- Fernández MH, Vrba ES (2005) A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biological Reviews* 80(2):269-302
- Fleagle JG (2013) *Primate Adaptation and Evolution*. Academic Press, Oxford
- Fleagle JG, Kay RF (1987) The phyletic position of the Parapithecidae. *Journal of Human Evolution* 16(6):483-532
- Fleagle JG, Kay RF (1994) Anthropoid origins. In: Ross CF, Kay RF (eds) *Anthropoid Origins*. Springer, New York, pp 675-698
- Fleagle JG, Tejedor MF (2002) Early platyrrhines of southern South America. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 161-173
- Ford SM (1980) Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in Platyrrhini. *Primates* 21(1):31-43

- Franzen JL, Gingerich PD, Habersetzer J, Hurum JH, von Koenigswald W, Smith BH (2009) Complete primate skeleton from the middle Eocene of Messel in Germany: morphology and paleobiology. *PLoS One* 4(5):e5723
- Fraser D, Rybczynski N (2014) Complexity of ruminant masticatory evolution. *Journal of Morphology* 275(10):1093-1102
- Frazier BC (2011) The cranial morphology of dwarf primate species. Doctoral Dissertation, Pennsylvania State University
- Garn SM, Koski K, Lewis AB (1957) Problems in determining the tooth eruption sequence in fossil and modern man. *American Journal of Physical Anthropology* 15(3):313-331
- Ge RL, Cai Q, Shen YY, San A, Lan M, Zhang Y, Yi X, Chen Y, Yang L, Huang Y, He R, Hui Y, Hao M, Li Y, Wang B, Ou X, Xu J, Zhang Y, Wu K, Geng C, Zhou W, Zhou T, Irwin D, Yang Y, Ying L, Bao H, Kim J, Larkin D, Ma J, Lewin H, Xing J, Platt II R, Ray D, Auvil L, Capitanu B, Zhang X, Zhang G, Murphy R, Wang J, Zhang Y, Wang J (2013) Draft genome sequence of the Tibetan antelope. *Nature Communications* 4:1-7
- Gebo DL (2002) Adapiformes: phylogeny and adaptation. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 21-44
- Geisler JH, Theodor JM, Uhen MD, Foss SE (2007) Phylogenetic relationships of cetaceans to terrestrial artiodactyls. In: Prothero DR, Foss S (eds) *The Evolution of Artiodactyla*. The John Hopkins University Press, Baltimore, pp 19-31
- Gentry AW (2000) The ruminant radiation. In: Vrba ES, Schaller GB (eds) *Antelopes, Deer, and Relatives*. Yale University Press, New Haven, pp 11-25
- Gentry AW, Heizmann EPJ (1996) Miocene ruminants of the central and eastern Tethys and Paratethys. In: Bernor R, Fahlbusch V, Mittmann H (eds) *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp 378-391
- Geraads D, Bobe R, Reed K (2012) Pliocene Bovidae (Mammalia) from the Hadar Formation of Hadar and Ledi-Geraru, Lower Awash, Ethiopia. *Journal of Vertebrate Paleontology* 32(1):180-197
- Gilbert C, Ropiquet A, Hassanin A (2006) Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): systematics, morphology, and biogeography. *Molecular Phylogenetics and Evolution* 40(1):101-117
- Gilbert WH (2003) *The Daka Member of the Bouri Formation, Middle Awash Valley, Ethiopia: Fauna, Stratigraphy, and Environment*. Doctoral Dissertation, University of California, Berkeley

- Gingerich PD (1974) Function of pointed premolars in *Phenacolemur* and other mammals. *Journal of Dental Research* 53:497
- Gingerich PD (1981) Early Cenozoic Omomyidae and the evolutionary history of tarsiiiform primates. *Journal of Human Evolution* 10(4):345-374
- Gingerich PD, Sahni A (1984) Dentition of *Sivaladapis nagrii* (Adapidae) from the late Miocene of India. *International Journal of Primatology* 5(1):63-79
- Godfrey LR, Jungers WI (2002) Quaternary fossil lemurs. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 97-122
- Godfrey LR, Samonds KE, Wright PC, King SJ (2005) Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. *Folia Primatologica* 76(2):77-99
- Godinot M (1994) Early North African primates and their significance for the origin of Simiiformes (= Anthropoidea). In: Fleagle JG, Kay RF (eds) *Anthropoid Origins*. Springer, New York, pp 235-295
- Godinot M (2006) Lemuriform origins as viewed from the fossil record. *Folia Primatologica* 77(6):446-464
- Goodman M, Czelusniak J, Page S, Meireles CL (2001) Where DNA sequence places *Homo sapiens* in a phylogenetic classification of primates. In: Tobias P, Raath M, Moogi-Cecchi J, Doyle G (eds) *Humanity from African Naissance to coming Millennia*. Firenze University Press, Johannesburg, pp 279-289
- Green MJB (1987) Scent-marking in the Himalayan musk deer (*Moschus chrysogaster*). *Journal of Zoology* 1:721-737
- Gregory WK (1920) On the structure and relations of *Notharctus*, an American Eocene primate. *Memoirs of the American Museum of Natural History NY*, 3(49)
- Grieco TM, Rizk OT, Hlusko LJ (2013) A modular framework characterizes micro- and macroevolution of old world monkey dentitions. *Evolution* 67(1):241-259
- Groves CP (1989) *A Theory of Human and Primate Evolution*. Oxford University Press, New York
- Groves CP (2001) *Primate taxonomy*. Smithsonian Books, Washington, DC
- Groves CP (2005) Order Primates. In: Wilson DE, Reeder DM (eds) *Mammal Species of the World*. The Johns Hopkins University Press, Baltimore, pp 111-184

- Groves CP, Shekelle M (2010) The genera and species of Tarsiidae. *International Journal of Primatology* 31(6):1071-1082
- Grzimek B (1990) *Grzimek's Animal Life Encyclopedia: Mammals I-IV*. McGraw-Hill Publishing Company, New York
- Gunnell GF, Rose KD (2002) Tarsiiformes: evolutionary history and adaptation. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 45-82
- Guthrie EH, Frost SR (2011) Pattern and pace of dental eruption in *Tarsius*. *American Journal of Physical Anthropology* 145(3):446-451
- Harrison T, Harris EE (1996) Plio-Pleistocene cercopithecids from Kanam East, western Kenya. *Journal of Human Evolution* 30:539-561
- Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge
- Hartwig WC, Meldrum DJ (2002) Miocene platyrrhines of the northern Neotropics. *Cambridge Studies In Biological And Evolutionary Anthropology*, pp 175-188.
- Harvati K (2000) Dental eruption sequence among colobine primates. *American Journal of Physical Anthropology* 112:69-85
- Harvati K, Frost SR (2007) Dental eruption sequences in fossil colobines and the evolution of primate life histories. *International Journal of Primatology* 28(3):705-728
- Harvey PH, Clutton-Brock TH (1985) Life history variation in primates. *Evolution* 559-581
- Hassanin, A, Delsuc F, Ropiquet A, Hammer C, van Vuuren BJ, Matthee C, Ruiz-Garcia M, Catzeflis F, Areskoug V, Nguyen TT, Couloux A (2012) Sequence and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies* 335(1):32-50
- Hassanin A, Douzery EJ (1999) The tribal radiation of the family Bovidae (Artiodactyla) and the evolution of the mitochondrial cytochrome *b* gene. *Molecular Phylogenetics and Evolution* 13(2):227-243
- Hassanin A, Pasquet E, Vigne JD (1998) Molecular systematics of the subfamily Caprinae (Artiodactyla, Bovidae) as determined from cytochrome *b* sequences. *Journal of Mammalian Evolution* 5(3):217-236
- Hellmund M (2013) Odontological and osteological investigations on propalaeotheriids (Mammalia, Equidae) from the Eocene Geiseltal Fossilagerstätte (Central Germany) - a full range of extraordinary phenomena. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 267:127-154

- Hellmund M (2016) Tooth emergence and replacement in the European *Hyrachyus minimus* (Fischer, 1829) (Mammalia, Perissodactyla) from the Geiseltal Fossilagerstätte—a further example for 'Schultz's rule' in ungulates. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 282(2):157-180
- Henderson E (2007) Platyrrhine dental eruption sequences. *American Journal of Physical Anthropology* 134(2):226-239
- Hiard F, Métais G, Goussard F (2014) On the “thumb” of anoplotheriins: a 3D comparative study of the hand of *Anoplotherium* and *Diplobune*. Swiss Geoscience Meeting, Platform Geosciences, Swiss Academy of Science, SCNAT
- Hill WCO (1954) *Man's Ancestry: A Primer of Human Phylogeny*. CC Thomas, Springfield, Illinois
- Hillson S (2005) *Teeth*. Cambridge University Press, Cambridge
- Hlusko LJ, Sage RD, Mahaney MC (2011) Modularity in the mammalian dentition: mice and monkeys share a common dental genetic architecture. *Journal of Experimental Zoology B: Molecular and Developmental Evolution* 316(1):21-49
- Hogue AS, Ravosa MJ (2001) Transverse masticatory movements, occlusal orientation, and symphyseal fusion in selenodont artiodactyls. *Journal of Morphology* 249(3):221-241
- Hooker JJ (2007) Bipedal browsing adaptations of the unusual Late Eocene - earliest Oligocene tylopod *Anoplotherium* (Artiodactyla, Mammalia). *Zoological Journal of the Linnean Society* 151(3):609-659
- Hylander WL, Ravosa MJ, Ross CF, Johnson KR (1998) Mandibular corpus strain in primates: further evidence for a functional link between symphyseal fusion and jaw-adductor muscle force. *American Journal of Physical Anthropology* 107(3):257-271
- Hylander WL, Ravosa MJ, Ross CF, Wall CE, Johnson KR (2000) Symphyseal fusion and jaw-adductor muscle force: an EMG study. *American Journal of Physical Anthropology* 112(4):469-492
- Hylander WL, Vinyard CJ, Ravosa MJ, Ross CR, Wall CE, Johnson KR (2004) Jaw adductor force and symphyseal fusion. In Anapol F, German R, Jablonski N (eds) *Shaping Primate Evolution: Papers in Honor of Charles Oxnard*. Cambridge University Press, Cambridge, pp 229-57
- Jablonski NG (1998) The evolution of the doucs and snub-nosed monkeys and the question of the phyletic unity of the odd-nosed colobines. In: Jablonski N (ed) *The Natural History of the Doucs and Snub-Nosed Monkeys*. World Scientific, Singapore, 13-52

- Jablonski NG (2002) Fossil Old World monkeys: the late Neogene radiation. In: Hartwig WC (ed) *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp 255-300
- Jablonski NG, Tyler DE (1999) *Trachypithecus auratus sangiranensis*, a new fossil monkey from Sangiran, Central Java, Indonesia. *International Journal of Primatology* 20(3):319-326
- Jameson NM, Hou ZC, Sterner KN, Weckle A, Goodman M, Steiper ME, Wildman DE (2011) Genomic data reject the hypothesis of a prosimian primate clade. *Journal of Human Evolution* 61(3):295-305
- Janis CM (1989) A climatic explanation for patterns of evolutionary diversity in ungulate mammals. *Palaeontology* 32(3):463-481
- Janis CM (1995) Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. In: Thomason J (ed) *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York, pp 76-98
- Järvinen E, Tummers M, Thesleff I (2009) The role of the dental lamina in mammalian tooth replacement. *Journal of Experimental Zoology B: Molecular and Developmental Evolution* 312(4):281-291
- Jogahara YO, Natori M (2012) Dental eruption sequence and eruption times in *Erythrocebus patas*. *Primates* 53(2):193-204
- Jones T, Ehardt CL, Butynski TM, Davenport TR, Mpunga NE, Machaga SJ, De Luca, DW (2005) The highland mangabey *Lophocebus kipunji*: a new species of African monkey. *Science* 308(5725):1161-1164
- Jordana X, Köhler M (2011) Enamel microstructure in the fossil bovid *Myotragus balearicus* (Majorca, Spain): implications for life-history evolution of dwarf mammals in insular ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology* 300(1):59-66
- Jordana X, Marín-Moratalla N, Moncunill-Solé B, Bover P, Alcover JA, Köhler M (2013) First fossil evidence for the advance of replacement teeth coupled with life history evolution along an anagenetic mammalian lineage. *PloS One* 8(7):e70743
- Jungers WL, Burr DB, Cole MS (1998) Body size and scaling of long bone geometry, bone strength, and positional behavior in cercopithecoid primates. In: Jungers W (ed) *Primate Locomotion*. Springer, New York, pp 309-330
- Kalb JE, Jaegar M, Jolly CJ, Kana B (1982a) Preliminary geology, palaeontology and paleoecology of a Sangoan site at Andalee, Middle Awash Valley, Ethiopia. *Journal of Archaeological Science* 9:349-363

- Kalb JE, Jolly CJ, Tebedge S, Mebrate A, Smart C, Oswald EB, Whitehead PF, Wood CB, Adefris T, Rawn-Schatzinger V (1982b) Vertebrate faunas from the Awash Group, Middle Awash Valley, Afar, Ethiopia. *Journal of Vertebrate Paleontology* 2(2):237-258
- Kay RF, Williams BA, Ross CF, Takai M, Shigehara N (2004) Anthropoid origins: a phylogenetic analysis. In Ross CF, Kay RF (eds) *Anthropoid Origins*. Springer, New York, pp 91-135
- Kay RF, Simons EL (1980) The ecology of Oligocene African Anthropoidea. *International Journal of Primatology* 1(1):21-37
- Kay RF, Simons EL (1983) Dental formulae and dental eruption patterns in Parapithecidae (Primates, Anthropoidea). *American Journal of Physical Anthropology* 62(4):363-375
- Kay RF, Ungar PS (1997) Dental evidence for diet in some Miocene catarrhines with comments on the effects of phylogeny on the interpretation of adaptation. In: Begun DR, Ward CV, Rose MD (eds) *Function, Phylogeny, and Fossils*. Springer, New York, pp 131-151
- Kellogg R (1936) A review of the Archaeoceti. *Carnegie Institution of Washington Publication* 482:366
- Kelley J, Smith TM (2003) Age at first molar emergence in early Miocene *Afropithecus turkanensis* and life-history evolution in the Hominoidea. *Journal of Human Evolution* 44(3):307-329
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463-1464
- Kerr GR (1966) *The ecology of mountain goats in west central Alberta*. Masters of Science Dissertation, University of Alberta (Calgary)
- Khan SM, Page S, Ahmad H, Ullah Z, Shaheen H, Ahmad M, Harper DM (2013) Phyto-climatic gradient of vegetation and habitat specificity in the high elevation western Himalayas. *Pakistan Journal of Botany* 45:223-230
- Kimbel WH, Johanson DC, Rak Y (1994) The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 368(6470):449-451
- Kjær I (2014) Mechanism of human tooth eruption: review article including a new theory for future studies on the eruption process. *Scientifica* pp 1-13
- Köhler M (1987) Boviden des türkischen Miozäns (Känozoikum und Braunkohlen der Türkei). *Paleontologia i Evolució* 21:133-246

- Köhler M, Moyà-Solà S (1999) A finding of Oligocene primates on the European continent. *Proceedings of the National Academy of Sciences* 96(25):14664-14667
- Köhler M, Moyà-Solà S (2009) Physiological and life history strategies of a fossil large mammal in a resource-limited environment. *Proceedings of the National Academy of Sciences* 106(48):20354-20358
- Kolnicki RL (1999) Karyotypic fission theory applied: kinetochore reproduction and lemur evolution. *Symbiosis* 26:123-141
- Koski K, Garn SM (1957) Tooth eruption sequence in fossil and modern man. *American Journal of Physical Anthropology* 15(4):469-488
- Kumar S, Hedges SB (1998) A molecular timescale for vertebrate evolution. *Nature* 392(6679):917-920
- Lalueza-Fox C, Castresana J, Sampietro L, Marquès-Bonet T, Alcover JA, Bertranpetit J (2005) Molecular dating of caprines using ancient DNA sequences of *Myotragus balearicus*, an extinct endemic Balearic mammal. *BMC Evolutionary Biology* 5:70-81
- Lamberton C (1938) Dentition de lait de quelques lemuriens subfossiles Malagaches. *Mammalia* 2:57-80
- Leigh SR, Setchell JM, Charpentier M, Knapp LA, Wickings EJ (2008) Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). *Journal of Human Evolution* 55(1):75-85
- Leslie Jr DM (2010) *Przewalskium albirostre* (Artiodactyla: Cervidae). *Mammalian Species* 42(1):7-18
- Lieberman DE, Crompton AW (2000) Why fuse the mandibular symphysis? A comparative analysis. *American Journal of Physical Anthropology* 112(4):517-540
- Loe LE, Meisingset EL, Mysterud A, Langvatn R, Stenseth NC (2004) Phenotypic and environmental correlates of tooth eruption in red deer (*Cervus elaphus*). *Journal of Zoology* 262(1):83-89
- Lohman DJ, de Bruyn M, Page T, von Rintelen K, Hall R, Ng PK, Shi HT, Carvalho GR, von Rintelen T (2011) Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics* 42:205-226
- Lucas SG, Schoch RM (1990) Ontogenetic studies of early Cenozoic *Coryphodon* (Mammalia, Pantodonta). *Journal of Paleontology* 831-841
- Macho GA, Williamson DK (2002) The effects of ecology on life history strategies and metabolic disturbances during development: an example from the African bovines. *Biological Journal of the Linnean Society* 75(2):271-279

- Maddison WP, Maddison DR (2015) Mesquite: a modular system for evolutionary analysis (Version 3.04). <http://mesquiteproject.org>
- Marks SC Jr (1973) Pathogenesis of osteopetrosis in the *ai* rat: reduced bone resorption due to reduced osteoclast function. *American Journal of Anatomy* 138:165-189
- Martin R (2004) Dermoptera (Colugos). In: Hutchins E, Thoney D, McDade M (eds) *Grzimek's Animal Life Encyclopedia, Vol. 13, 2nd Edition*. Gale, Detroit, pp 299-305
- Masters JC, Silvestro D, Génin F, DelPero M (2013) Seeing the wood through the trees: the current state of higher systematics in the Strepsirhini. *Folia Primatologica* 84(3-5):201-219
- Mathee CA, Burzlaff JD, Taylor JF, Davis SK (2001) Mining the mammalian genome for artiodactyl systematics. *Systematic Biology* 50(3):367-390
- McCann K (2009) "*Perodicticus potto*" (On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Perodicticus_potto/
- McCollum M, Sharpe PT (2001) Evolution and development of teeth. *Journal of Anatomy* 199:153-159
- McGee EM, Turnbull WD (2010) A paleopopulation of *Coryphodon lobatus* (Mammalia: Pantodonta) from Deardorff Hill Coryphodon Quarry, Piceance Creek Basin, Colorado. *Fieldiana: Geology, NS* 52:1-12
- McGuinness R (2011) "*Loris tardigradus*" (On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Loris_tardigradus/
- McKenna MC, Bell SK (1997) *Classification of Mammals: Above the Species Level*. Columbia University Press, New York
- Medway L (1970) Breeding of the silvered leaf monkey, *Presbytis cristata*, in Malaya. *Journal of Mammalogy* 51(3):630-632
- Meredith R, Janečka J, Gatesy J, Ryder O, Fisher C, Teeling E, Goodbla A, Eizirik E, Simão T, Stadler T, Rabosky D, Honeycutt R, Flynn J, Ingram C, Steiner C, Williams T, Robinson T, Burk-Herrick A, Westerman M, Ayoub N, Springer M, Murphy W (2011) Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334(6055):521-524
- Merker S, Groves CP (2006) *Tarsius lariang*: a new primate species from western central Sulawesi. *International Journal of Primatology* 27(2):465-485
- Métais G, Vislobokova N (2007) Basal ruminants. In: Prothero DR, Foss S (eds) *The Evolution of Artiodactyla*. The John Hopkins University Press, Baltimore, pp 189-212

- Meyer D, Rinaldi ID, Ramlee H, Perwitasari-Farajallah D, Hodges JK, Roos C (2011) Mitochondrial phylogeny of leaf monkeys (genus *Presbytis*, Eschscholtz, 1821) with implications for taxonomy and conservation. *Molecular Phylogenetics and Evolution* 59(2):311-319
- Mittermeier RA, Coimbra-Filho AF (1977) Primate conservation in Brazilian Amazonia. In: Prince Rainier III HSH, Bourne GH (eds) *Primate Conservation*, Academic Press, New York, pp 117-166
- Mittermeier RA, Rylands AB, Konstant WR (1999) Primates of the World: An Introduction. In: Nowak RM (ed) *Primates of the World*, The Johns Hopkins University Press, Baltimore, pp 1-52
- Monson TA, Brasil MF, Hlusko LJ (2015) Materials collected by the southern branch of the UC Africa Expedition with a report on previously unpublished Plio-Pleistocene fossil localities. *PaleoBios* 32(1):1-17
- Monson TA, Hlusko LJ (2016) The evolution of dental eruption sequence in artiodactyls. *Journal of Mammalian Evolution* 1:1-12
- Molvar E, Bowyer R, Van Ballenberghe V (1993) Moose herbivory, browse quality and nutrient cycling in an Alaskan tree line community. *Oecologia* 94:472-479
- Morales-Jimenez AL, Disotell T, Di Fiore A (2015) Revisiting the phylogenetic relationships, biogeography, and taxonomy of spider monkeys (genus *Ateles*) in light of new molecular data. *Molecular Phylogenetics and Evolution* 82:467-483
- Murphy WJ, Eizirik E, Johnson WE, Zhang YP, Ryder OA, O'Brien SJ (2001) Molecular phylogenetics and the origins of placental mammals. *Nature* 409(6820):614-618
- Nowak RN (1999) *Walker's Primates of the World*. The Johns Hopkins University Press, Baltimore
- Opazo JC, Wildman DE, Prychitko T, Johnson RM, Goodman M (2006) Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). *Molecular Phylogenetics and Evolution* 40(1):274-280
- Oppenheimer JR (1977) *Presbytis entellus*, the Hanuman langur. In: Prince Rainier III HSH, Bourne GH (eds) *Primate Conservation*. Academic Press, New York, pp 469-512
- Orliac MC, Brualla N, Assemat A, Guignard M, Lihoreau F (2016) Hooves on the roof: the ear region of *Diplobune minor*, an arboreal artiodactyl from the Early Oligocene of France. *The 11th International Congress of Vertebrate Morphology*, Bethesda, MD
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W (2015) The *capre* package: comparative analysis of phylogenetics and evolution in R. *R package version 5(2)*

- Osborn JW, Crompton AW (1973) The evolution of mammalian from reptilian dentitions. *Breviora* 399:1-18
- Owen-Smith N, Fryxell JM, Merrill EH (2010) Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1550):2267-2278
- Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20(2):289-290
- Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, Moreira MAM, Kessing B, Pontius J, Roelke M, Rumpler Y, Schneider MPC, Silva A, O'Brien SJ, Pecon-Slattery J (2011) A molecular phylogeny of living primates. *PLoS Genetics* 7:e1001342-10.1371/journal.pgen.1001342
- Perry JM, Kay RF, Vizcaíno SF, Bargo MS (2014) Oldest known cranium of a juvenile New World monkey (Early Miocene, Patagonia, Argentina): implications for the taxonomy and the molar eruption pattern of early platyrrhines. *Journal of Human Evolution* 74:67-81
- Phillips EM, Walker AC (2000) A new species of fossil loroid from the Miocene of East Africa. *Primates* 41:367-372
- Poux C, Douzery EJ (2004) Primate phylogeny, evolutionary rate variations, and divergence times: a contribution from the nuclear gene IRBP. *American Journal of Physical Anthropology* 124(1):1-16
- Pozzi L, Hodgson JA, Burrell AS, Sterner KN, Raaum RL, Disotell TR (2014) Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. *Molecular Phylogenetics and Evolution* 75:165-183
- Prothero DR, Foss SE (2007) *The Evolution of Artiodactyls*. The Johns Hopkins University Press, Baltimore
- R Core Team (2016) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, <http://www.R-project.org/>
- Radinsky L (1985) Patterns in the evolution of ungulate jaw shape. *American Zoologist* 303-314
- Rasmussen DT, Simons EL (1992) Paleobiology of the Oligopithecines, the earliest known anthropoid primates. *International Journal of Primatology* 13:477-508
- Ravosa MJ (1996) Mandibular form and function in North American and European Adapidae and Omomyidae. *Journal of Morphology* 229(2):171-190

- Ravosa M (1999) Anthropoid origins and the modern symphysis. *Folia Primatologica* 70(2):65-78
- Ravosa MJ, Hogue AS (2004) Function and fusion of the mandibular symphysis in mammals: a comparative and experimental perspective. In: Fleagle JG, Kay RF (eds) *Anthropoid Origins* Springer, New York, pp 413-462
- Reif WE (1982) Evolution of dermal skeleton and dentition in vertebrates. In: Hecht MK, Wallace B, Prance GT (eds) *Evolutionary Biology*. Plenum Press, New York, pp 287-368
- Revell LJ, Harmon LJ, Collar DC (2008) Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* 57(4):591-601
- Ricklefs RE, Starck JM (1996) Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos* 77(1):167-172
- Robson SL, Wood B (2008) Hominin life history: reconstruction and evolution. *Journal of Anatomy* 212(4):394-425
- Roos C, Schmitz J, Zischler H (2004) Primate jumping genes elucidate strepsirrhine phylogeny. *Proceedings of the National Academy of Sciences* 101(29):10650-10654
- Ropiquet A, Hassanin A (2005) Molecular evidence for the polyphyly of the genus *Hemitragus* (Mammalia, Bovidae). *Molecular Phylogenetics and Evolution* 36(1):154-168
- Ropiquet A, Hassanin A (2006) Hybrid origin of the Pliocene ancestor of wild goats. *Molecular Phylogenetics and Evolution* 41(2):395-404
- Rosenberger AL, Hartwig WC (2013) Primates (Lemurs, Lorises, Tarsiers, Monkeys and Apes). *Encyclopedia of Life Sciences*. John Wiley & Sons, Ltd, Chichester
- Roycewicz J (2001) "*Eulemur mongoz*" (On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Eulemur_mongoz/
- Rylands AB, Mittermeier RA (2014) Primate taxonomy: species and conservation. *Evolutionary Anthropology: Issues, News, and Reviews* 23(1):8-10
- Sacher GA (1959) Relation of lifespan to brain weight and body weight in mammals. In: Wolstenholme GEW, O'Connor M (eds) *The Lifespan of Animals, CIBA Foundation Colloquia on Ageing Volume 5*, pp 115-41
- Sacher GA (1975) Maturation and longevity in relation to cranial capacity in hominid evolution. In: Tuttle RH (ed) *Primate Functional Morphology and Evolution*. Mouton, The Hague
- Sacher GA (1978) Longevity, aging, and death: an evolutionary perspective. *Gerontology* 18:112-119

- Sacher GA, Staffeldt EF (1974) Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. *American Naturalist* 108:593-616
- Schmitz J, Ohme M, Zischler H (2001) SINE insertions in cladistic analyses and the phylogenetic affiliations of *Tarsius bancanus* to other primates. *Genetics* 157(2):777-784
- Schmitz J, Ohme M, Zischler H (2002) The complete mitochondrial sequence of *Tarsius bancanus*: evidence for an extensive nucleotide compositional plasticity of primate mitochondrial DNA. *Molecular Biology and Evolution* 19(4):544-553
- Schneider H, Sampaio I (2015) The systematics and evolution of New World primates—A review. *Molecular Phylogenetics and Evolution* 82:348-357
- Schultz AH (1935) Eruption and decay of the permanent teeth in primates. *American Journal of Physical Anthropology* 19(1):489-581
- Schultz AH (1950) The physical distinctions of man. *Proceedings of the American Philosophical Society* 94(5):428-449
- Schultz AH (1956) Postembryonic age changes. In: Hofer H, Schultz AH, Starck D (eds) *Primatologia*. Karger, Basel, pp 887-964
- Schultz AH (1960) Age changes in primates and their modification in man. In: Tanner JM (ed) *Human Growth Vol III*. Pergamon Press, Oxford, pp 1-20
- Schwartz JH (1974) *Dental development and eruption in the prosimians and its bearing on their evolution*. Doctoral Dissertation, Columbia University
- Schwartz GT, Mahoney P, Godfrey LR, Cuzzo FP, Jungers WL, Randria GF (2005) Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): implications for understanding life history variation in subfossil lemurs. *Journal of Human Evolution* 49(6):702-721
- Scott JE (2015) Lost and found: the third molars of *Callimico goeldii* and the evolution of the callitrichine postcanine dentition. *Journal of Human Evolution* 83:65-73
- Seiffert ER, Perry JM, Simons EL, Boyer DM (2009) Convergent evolution of anthropoid-like adaptations in Eocene adapiform primates. *Nature* 461(7267):1118-1121
- Seiffert ER, Simons EL, Attia Y (2003) Fossil evidence for an ancient divergence of lorises and galagos. *Nature* 422(6930):421-424
- Seiffert ER, Simons EL, Ryan TM, Attia Y (2005) Additional remains of *Wadilemur elegans*, a primitive stem galagid from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences* 102(32):11396-11401

- Şenyürek M (1955) A review of the order of eruption of the permanent teeth in fossil hominids. *Türk Tarih Kurumu Belleten* 19:407-444
- Setoguchi T, Rosenberger AL (1987) A fossil owl monkey from La Venta, Colombia. *Nature* 326:692-694
- Shafer A, Hall J (2010) Placing the mountain goat: a total evidence approach to testing alternative hypotheses. *Molecular Phylogenetics and Evolution* 55(1):18-25
- Shaheen H, Shinwari ZK (2012) Phyto diversity and endemic richness of Karambar Lake Vegetation from Chitral, Hindukush-Himalayas. *Pakistan Journal of Botany* 44(1):17-21
- Shekelle M, Meier R, Wahyu I, Ting N (2010) Molecular phylogenetics and chronometrics of Tarsiidae based on 12S mtDNA haplotypes: evidence for Miocene origins of crown tarsiers and numerous species within the Sulawesi clade. *International Journal of Primatology* 31(6):1083-1106
- Shi R, Sun Y, Teng L, Liu Z (2016) Complete mitochondrial genome of red goral (*Naemorhedus baileyi*) and a complete estimate of the phylogenetic relationships in Caprinae. *Mitochondrial DNA Part A* 27(4):2721-2722
- Simons EL (1976) The fossil record of primate phylogeny. In: Goodman M, Tashian RE, Tashian JH (eds) *Molecular Anthropology*. Springer, New York, pp 35-62
- Simons EL (1989) Description of two genera and species of Late Eocene Anthropoidea from Egypt. *Proceedings of the National Academy of Sciences* 86:9956-9960
- Simons EL, Rasmussen DT (1989) Cranial morphology of *Aegyptopithecus* and *Tarsius* and the question of the tarsier-anthropean clade. *American Journal of Physical Anthropology* 79(1):1-23
- Simons EL, Rasmussen T (1994) A whole new world of ancestors: Eocene anthropoideans from Africa. *Evolutionary Anthropology: Issues, News, and Reviews* 3(4):128-139
- Smith BH (1989) Dental development as a measure of life history in primates. *Evolution* 43(3):683-688
- Smith BH (1991) Dental development and the evolution of life history in Hominidae. *American Journal of Physical Anthropology* 86(2):157-174
- Smith BH (1994) Sequence of emergence of the permanent teeth in *Macaca*, *Pan*, *Homo*, and *Australopithecus*: its evolutionary significance. *American Journal of Human Biology* 6:61-76
- Smith BH (2000) 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. In: Teaford MF, Smith MM, Ferguson MW (eds) *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge, pp 212-227

- Smith BH, Crummett TL, Brandt KL (1994) Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. *American Journal of Physical Anthropology* 37(S19):177-231
- Smith GE (1919) Discussion on the zoological position and affinities of *Tarsius*. *Proceedings of the Zoological Society of London* 1919:465-475
- Smith MM, Coates MI (2001) Evolutionary origins of teeth and jaws: developmental models and phylogenetic patterns. In: Teaford MF, Smith MM, Ferguson MW (eds) *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge
- Smith MM, Hall BK (1993) A developmental model for evolution of the vertebrate exoskeleton and teeth. In: Hecht MK, Wallace B, Prance GT (eds) *Evolutionary Biology*. Plenum Press, New York, pp 387-448
- Smith R (2015) "*Nycticebus bengalensis*" (On-line), Animal Diversity Web. <http://animaldiversity.org/accounts>
- Smith RJ, Gannon PJ, Smith BH (1995) Ontogeny of australopithecines and early *Homo*: evidence from cranial capacity and dental eruption. *Journal of Human Evolution* 29(2):155-168
- Smith RJ, Jungers WL (1997) Body mass in comparative primatology. *Journal of Human Evolution* 32(6):523-559
- Soligo C, Will OA, Tavaré S, Marshall CR, Martin RD (2007) New light on the dates of primate origins and divergence. In: Ravosa MJ, Dagosta M (eds) *Primate Origins: Adaptations and Evolution*. Springer, New York, pp 29-49
- Spaulding M, O'Leary MA, Gatesy J (2009) Relationships of Cetacea (Artiodactyla) among mammals: increased taxon sampling alters interpretations of key fossils and character evolution. *Plos One* 4(9):e7062
- Steiper ME, Young NM (2006) Primate molecular divergence dates. *Molecular Phylogenetics and Evolution* 41(2):384-394
- Sterner KN, Raaum RL, Zhang YP, Stewart CB, Disotell TR (2006) Mitochondrial data support an odd-nosed colobine clade. *Molecular Phylogenetics and Evolution* 40:1-7
- Strömberg CA (2011) Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences* 39:517-544
- Sudre J (1974) D'importantes restes de *Diplobune minor* Filhol à Itardies (Quercy). *Palaeovertebrata* 6:47-54

- Sudre J (1983) Interprétation de la denture et description des éléments du squelette appendiculaire de l'espèce *Diplobune minor* (Filhol, 1877): apports à la connaissance de l'anatomie des Anoplotheriinae Bonaparte, 1850. In: Buffetaut E, Mazin JM, Salmon E, (eds) *Actes du Symposium Paléontologique G Cuvier*. Montbeliard, La Ville de Montbeliard, pp 439-458
- Suri L, Gagari E, Vastardis H (2004) Delayed tooth eruption: pathogenesis, diagnosis, and treatment. *American Journal of Orthodontics and Dentofacial Orthopedics* 126(4):432-445
- Swindler DR (2002) *Primate Dentition*. Cambridge University Press, Cambridge
- Szalay FS, Delson E (1979) *Evolutionary History of the Primates*. Academic Press, San Diego
- Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, Taranukha D, Costa J, Fraifeld VE, de Magalhaes JP (2013) Human Ageing Genomic Resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic Acids Research* 41(D1):D1027-D1033
- Tattersall I (1973) *Cranial Anatomy of the Archaeolemurinae (Lemuroidea, Primates)* (Vol. 52). American Museum of Natural History 52(1):1-110
- Tattersall I (1974) Facial structure and mandibular mechanics in *Archaeolemur*. In: Martin R, Doyle G, Walker A (eds) *Prosimian Biology*. University of Pittsburgh Press, Pittsburgh, pp 563-577
- Tattersall I, Schwartz JH (1974) Craniodental morphology and the systematics of the Malagasy lemurs (Primates, Prosimii). *Anthropological Papers of the American Museum of Natural History* 52:139-192
- Theodor JM, Erfurt J, Métais G (2007) The earliest artiodactyls. In: Prothero DR, Foss S (eds) *The Evolution of Artiodactyla*. The John Hopkins University Press, Baltimore, pp 32-58
- Townsend B, Croft DA (2010) Middle Miocene mesotheriine diversity at Cerdas, Bolivia and a reconsideration of *Plesiotypotherium minus*. *Palaeontologia Electronica* 13(1):1-36
- Tranquillini W (1964) The physiology of plants at high altitudes. *Annual Review of Plant Biology* 15(1):345-362
- Tsujikawa H (2005) The updated late Miocene large mammal fauna from Samburu Hills, northern Kenya. *African Study Monographs Supplement* 32:1-50
- Tummers M, Thesleff I (2009) The importance of signal pathway modulation in all aspects of tooth development. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 312(4):309-319
- Ungar PS (2010) *Mammal Teeth*. The Johns Hopkins University Press, Baltimore

- Van Nievelt AF, Smith KK (2005) Tooth eruption in *Monodelphis domestica* and its significance for phylogeny and natural history. *Journal of Mammalogy* 86(2):333-341
- Vázquez GJA, Givnish TJ (1998) Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* 86(6):999-1020
- Veitschegger K, Sánchez-Villagra MR (2016) Tooth eruption sequences in cervids and the effect of morphology, life history, and phylogeny. *Journal of Mammalian Evolution* 23:251-263
- Vrba ES (1997) New fossils of Alcelaphini and Caprinae (Bovidae: Mammalia) from Awash, Ethiopia, and phylogenetic analysis of Alcelaphini. *Palaeontologia Africana* 34:127-198
- Vrba ES, Schaller GB (2000a) Introduction. In: Vrba ES, Schaller GB (eds) *Antelopes, Deer, and Relatives*. Yale University Press, New Haven, pp 1-10
- Vrba ES, Schaller GB (2000b) Phylogeny of bovidae based on behavior, glands, skulls and postcrania. In: Vrba ES, Schaller GB (eds) *Antelopes, Deer, and Relatives*. Yale University Press, New Haven, pp 203-222
- Vun VF, Mahani MC, Lakim M, Ampeng A, Md-Zain BM (2011) Phylogenetic relationships of leaf monkeys (*Presbytis*; Colobinae) based on cytochrome b and 12S rRNA genes. *Genetics and Molecular Research* 10(1):368-381
- Wallace JA (1977) Gingival eruption sequences of permanent teeth in early hominids. *American Journal of Physical Anthropology* 46(3):483-493
- White TD, Suwa G, Simpson S, Asfaw B (2000) Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *American Journal of Physical Anthropology* 111(1):45-68
- Williams BA, Kay RF, Kirk EC (2010) New perspectives on anthropoid origins. *Proceedings of the National Academy of Sciences* 107(11):4797-4804
- Willis MS, Swindler DR (2004) Molar size and shape variations among Asian colobines. *American Journal of Physical Anthropology* 125(1):51-60
- Wise GE, Frazier-Bowers S, D'souza RN (2002) Cellular, molecular, and genetic determinants of tooth eruption. *Critical Reviews in Oral Biology and Medicine* 13(4):323-335
- Wolfe JA (1985) Distribution of major vegetational types during the Tertiary. In: Sundquist ET, Broecker WS (eds) *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archean to Present*. American Geophysical Union, Washington, DC, pp 357-375
- Woodroffe S, Mihailidis S, Hughes T, Bockmann M, Seow WK, Gotjamanos T, Townsend G (2010) Primary tooth emergence in Australian children: timing, sequence and patterns of asymmetry. *Australian Dental Journal* 55(3):245-251

- Yamanaka A, Yasui K, Sonomura T, Iwai H, Uemura M (2010) Development of deciduous and permanent dentitions in the upper jaw of the house shrew (*Suncus murinus*). *Archives of Oral Biology* 55(4):279-287
- Yoder AD, Yang Z (2004) Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Molecular Ecology* 13(4):757-773
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292(5517):686-693
- Zhou L, Su YC, Thomas DC, Saunders RM (2012) 'Out-of-Africa' dispersal of tropical floras during the Miocene climatic optimum: evidence from *Uvaria* (Annonaceae). *Journal of Biogeography* 39(2):322-335
- Zhou X, Xu S, Yang Y, Zhou K, Yang G (2011) Phylogenomic analyses and improved resolution of Cetartiodactyla. *Molecular Phylogenetics and Evolution* 61(2):255-264

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
4737	<i>O. dalli</i>	0	2	3	0	0	0	0	0	0	3	2	0
97810	<i>O. canadensis</i>	0	0	3	0	0	0	0	0	0	3	0	0
112003	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
145654	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145650	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145652	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145646	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145648	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188107	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188089	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
77265	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188082	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
2320	<i>O. canadensis</i>	1	2	3	0	0	0	0	0	0	3	2	1
24533	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
25819	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
76264	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
186317	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
185201	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
185200	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
185183	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
185184	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
185182	<i>O. canadensis</i>	1	3	3	0	0	0	0	0	0	3	3	1
145655	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145141	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145636	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
16358	<i>O. canadensis</i>	1	3	3	0	0	0	0	0	0	3	3	1

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data, continued*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
16359	<i>O. canadensis</i>	1	3	3	0	0	0	0	0	0	3	3	1
185198	<i>O. canadensis</i>	1	3	3	0	0	0	0	0	0	3	3	1
185181	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1034	<i>O. canadensis</i>	1	3	3	1	1	1	1	1	1	3	3	1
185197	<i>O. canadensis</i>	1	3	3	0	0	0	0	0	0	3	3	1
70205	<i>O. canadensis</i>	2	3	3	1	2	2	2	2	1	3	3	1
2319	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
185199	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145659	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145637	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145635	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
16357	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
119468	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
188106	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188100	<i>O. canadensis</i>	2	3	3	3	3	3	3	3	3	3	3	2
3251	<i>O. canadensis</i>	2	3	3	3	3	3	3	3	3	3	3	2
61917	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
94723	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
76232	<i>O. canadensis</i>	NA											0
186316	<i>O. canadensis</i>	2	3	3	3	3	3	3	3	3	3	3	2
93851	<i>O. dalli</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
181222	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
4360	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
97809	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
89270	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
47237	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data, continued*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
97811	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
112004	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
112002	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
137894	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
137893	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145658	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145657	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145621	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
145639	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145638	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145640	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145643	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145644	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145625	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145627	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145629	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145631	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145633	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145626	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145628	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145623	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145624	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
34172	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
31827	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
40887	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
93097	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data, continued*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
90623	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
132219	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
4751	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
71803	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188103	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
3252	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188096	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1030	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1031	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188097	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188095	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188094	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188093	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188092	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188088	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
24413	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
81967	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
80659	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
77741	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188085	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188086	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188084	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188080	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188081	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188079	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188076	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data, continued*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
188077	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
33477	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
154262	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
41460	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
414106	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
3485	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
134117	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
134135	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188075	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
24532	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188074	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188078	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188072	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188073	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188070	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188069	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
84251	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
4739	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
4738	<i>O. dalli</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
96105	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
4764	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
134118	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188068	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
184165	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145660	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
10593	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data, continued*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
10592	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
21436	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
10588	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
84250	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
76230	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
88136	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
96104	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78270	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
77357	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
70359	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
70358	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78269	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78268	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78267	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78266	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78265	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78262	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78261	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78260	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78259	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78258	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
4375	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186314	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186319	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186318	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186315	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data, continued*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
170008	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170009	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170007	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
70004	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170001	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170002	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170003	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170000	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170005	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
169998	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
169999	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
42087	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
38899	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185196	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185198	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185194	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185192	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185193	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
15190	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185188	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185189	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
85187	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
22932	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
38986	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
125586	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
188104	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix A Test of intraspecific variation in *Ovis*, mandibular raw data, continued*

ID	Species	LM ₃	LM ₂	LM ₁	LP ₄	LP ₃	LP ₂	RP ₂	RP ₃	RP ₄	RM ₁	RM ₂	RM ₃
47327	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78263	<i>O. canadensis</i>	0	1	2	0	0	0	0	0	0	2	1	0
185185	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0

*L is left, R is right, M is molar, P is premolar, subscript indicates mandibular tooth number, e.g., LM₂ is left mandibular second molar. See Chapter 3 for methods

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
4737	<i>O. dalli</i>	0	2	3	0	0	0	0	0	0	3	2	0
97810	<i>O. canadensis</i>	0	0	2	0	0	0	0	0	0	2	0	0
112003	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
145654	<i>O. canadensis</i>	0	0	1	0	0	0	0	0	0	1	0	0
145650	<i>O. canadensis</i>	0	0	2	0	0	0	0	0	0	2	0	0
145652	<i>O. canadensis</i>	0	0	1	0	0	0	0	0	0	1	0	0
145646	<i>O. canadensis</i>	0	1	2	0	0	0	0	0	0	2	1	0
145648	<i>O. canadensis</i>	0	0	1	0	0	0	0	0	0	1	0	0
188107	<i>O. canadensis</i>	0	0	1	0	0	0	0	0	0	1	0	0
188089	<i>O. canadensis</i>	0	0	1	0	0	0	0	0	0	1	0	0
77265	<i>O. canadensis</i>	0	0	2	0	0	0	0	0	0	2	0	0
188082	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
2320	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
24533	<i>O. canadensis</i>	0	1	3	0	0	0	0	0	0	3	1	0
25819	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
76264	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
186317	<i>O. canadensis</i>	0	1	3	0	0	0	0	0	0	3	1	0
185201	<i>O. canadensis</i>	0	1	2	0	0	0	0	0	0	2	1	0
185200	<i>O. canadensis</i>	0	1	3	0	0	0	0	0	0	3	1	0
185183	<i>O. canadensis</i>	0	1	3	0	0	0	0	0	0	3	1	0
185184	<i>O. canadensis</i>	0	2	3	0	0	0	0	0	0	3	2	0
185182	<i>O. canadensis</i>	0	3	3	0	0	0	0	0	0	3	3	0
145655	<i>O. canadensis</i>	1	2	3	0	0	0	0	0	0	3	2	1
145141	<i>O. canadensis</i>	1	2	3	0	0	0	0	0	0	3	2	1
145636	<i>O. canadensis</i>	1	2	3	0	0	0	0	0	0	3	2	1
16358	<i>O. canadensis</i>	1	2	3	0	0	0	0	0	0	3	2	1

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data, continued*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
16359	<i>O. canadensis</i>	1	2	3	0	0	0	0	0	0	3	2	1
185198	<i>O. canadensis</i>	1	3	3	0	0	0	0	0	0	3	3	1
185181	<i>O. canadensis</i>	1	3	3	0	0	0	0	0	0	3	3	1
1034	<i>O. canadensis</i>	1	3	3	0	1	1	1	1	0	3	3	1
185197	<i>O. canadensis</i>	1	3	3	0	0	1	1	0	0	3	3	1
70205	<i>O. canadensis</i>	1	3	3	1	2	2	2	2	1	3	3	1
2319	<i>O. canadensis</i>	2	3	3	2	2	2	2	2	2	3	3	2
185199	<i>O. canadensis</i>	2	3	3	2	2	2	2	2	3	3	3	2
145659	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
145637	<i>O. canadensis</i>	2	3	3	3	3	3	3	3	3	3	3	2
145635	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
16357	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
119468	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
188106	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
188100	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
3251	<i>O. canadensis</i>	2	3	3	2	3	3	3	3	2	3	3	2
61917	<i>O. canadensis</i>	2	3	3	3	3	3	3	3	3	3	3	2
94723	<i>O. canadensis</i>	2	3	3	3	3	3	3	3	3	3	3	2
76232	<i>O. canadensis</i>	2	3	3	2	3	3	2	3	3	2	3	3
186316	<i>O. canadensis</i>	2	3	3	3	3	3	3	3	3	3	3	2
93851	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
181222	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
4360	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
97809	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
89270	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
47237	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data, continued*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
97811	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
112004	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
112002	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
137894	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
137893	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145658	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145657	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145621	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145639	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145638	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145640	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145643	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145644	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145625	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145627	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145629	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145631	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145633	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145626	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145628	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145623	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145624	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
34172	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
31827	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
40887	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
93097	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data, continued*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
90623	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
132219	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
4751	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
71803	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188103	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
3252	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188096	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
1030	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
1031	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188097	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188095	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188094	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188093	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188092	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188088	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
24413	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
81967	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
80659	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
77741	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188085	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188086	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188084	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188080	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188081	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188079	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188076	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data, continued*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
188077	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
33477	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
154262	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
41460	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
414106	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
3485	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
134117	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
134135	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188075	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
24532	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188074	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188078	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188072	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188073	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188070	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188069	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
84251	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
4739	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
4738	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
96105	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
4764	<i>O. dalli</i>	3	3	3	3	3	3	3	3	3	3	3	3
134118	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
188068	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
184165	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
145660	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
10593	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data, continued*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
10592	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
21436	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
10588	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
84250	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
76230	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
88136	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
96104	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78270	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
77357	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
70359	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
70358	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78269	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78268	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78267	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78266	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78265	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78262	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78261	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78260	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78259	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
78258	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
4375	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186314	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186319	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186318	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
186315	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data, continued*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
170008	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170009	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170007	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
70004	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170001	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170002	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170003	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170000	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
170005	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
169998	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
169999	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
42087	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
38899	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185196	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185198	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185194	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185192	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185193	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
15190	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185188	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
185189	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
85187	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
22932	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
38986	<i>O. canadensis</i>	3	3	3	3	3	3	3	3	3	3	3	3
125586	<i>O. dalli</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
188104	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix B Test of intraspecific variation in *Ovis*, maxillary raw data, continued*

ID	Species	LM ³	LM ²	LM ¹	LP ⁴	LP ³	LP ²	RP ²	RP ³	RP ⁴	RM ¹	RM ²	RM ³
47327	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
78263	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
185185	<i>O. canadensis</i>	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

*L is left, R is right, M is molar, P is premolar, superscript indicates maxillary tooth number, e.g., LM² is left maxillary second molar. See Chapter 3 for methods

Appendix C Life history and body size variables for the primate sample, raw data*

Family	Genus	Species	PM before M3	Max Lifespan	Body Mass (F, kg)	Age at Weaning (mos)	Gestation (days)	Litter size	Age at Sexual Maturity (F, yrs)
Cercopithecidae	<i>Allenopithecus</i>	<i>nigroviridis</i>	YES	27.00	5.50	2.50	NA	1	NA
Cercopithecidae	<i>Cercocebus</i>	<i>agilis</i>	YES	21.00	5.26	NA	169.50	1	4.72
Cercopithecidae	<i>Cercocebus</i>	<i>torquatus</i>	YES	46.00	5.50	NA	171.55	1	2.67
Cercopithecidae	<i>Cercopithecus</i>	<i>aethiops</i>	YES	30.80	3.56	6.00	165.00	1	2.50
Cercopithecidae	<i>Colobus</i>	<i>angolensis</i>	YES	35.30	7.57	NA	175.00	1	3.00
Cercopithecidae	<i>Colobus</i>	<i>guereza</i>	YES	35.00	9.20	12.96	175.00	1	4.00
Cercopithecidae	<i>Colobus</i>	<i>polykomos</i>	YES	33.90	8.30	9.00	170.00	1	4.50
Cercopithecidae	<i>Colobus</i>	<i>satanas</i>	YES	NA	7.42	NA	195.00	1	NA
Cercopithecidae	<i>Colobus</i>	<i>vellerosus</i>	YES	NA	6.90	27.37	NA	NA	NA
Cercopithecidae	<i>Erythrocebus</i>	<i>patas</i>	YES	28.30	6.50	5.40	167.00	1	2.50
Cercopithecidae	<i>Lophocebus</i>	<i>albigena</i>	YES	36.00	6.02	7.77	174.00	1	4.00
Cercopithecidae	<i>Macaca</i>	<i>mulatta</i>	YES	40.00	5.24	13.08	166.00	1	3.25
Cercopithecidae	<i>Miopithecus</i>	<i>talapoin</i>	YES	27.70	1.12	4.33	162.00	1	4.50
Cercopithecidae	<i>Nasalis</i>	<i>larvatus</i>	YES	25.10	9.83	9.24	166.00	1	4.00
Cercopithecidae	<i>Papio</i>	<i>hamadryas</i>	YES	37.50	12.50	14.00	171.50	1	5.00
Cercopithecidae	<i>Ptilocolobus</i>	<i>badius</i>	YES	NA	NA	NA	NA	NA	NA
Cercopithecidae	<i>Procolobus</i>	<i>verus</i>	YES	NA	8.21	NA	180.00	1	NA
Cercopithecidae	<i>Pygathrix</i>	<i>nemaus</i>	YES	26.00	8.06	11.04	177.50	1	4.00
Cercopithecidae	<i>Semnopithecus</i>	<i>entellus</i>	NO	29.00	11.00	11.00	200.00	1	3.50
Cercopithecidae	<i>Trachypithecus</i>	<i>cristatus</i>	YES	28.30	5.76	12.00	180.00	1	3.50
Cercopithecidae	<i>Trachypithecus</i>	<i>phayrei</i>	YES	28.30	6.30	12.00	167.00	1	NA

Appendix C Life history and body size variables for the primate sample, raw data, continued*

Family	Genus	Species	PM before M3	Max Lifespan	Body Mass (F, kg)	Age at Weaning (mos)	Gestation (days)	Litter size	Age at Sexual Maturity (F, yrs)
Gorillidae	<i>Gorilla</i>	<i>gorilla</i>	YES	55.40	75.50	42.00	273.00	1	8.00
Hominidae	<i>Homo</i>	<i>sapiens</i>	YES	122.50	56.30	21.30	280.00	1	13.00
Hylobatidae	<i>Hylobates</i>	<i>agilis</i>	YES	49.00	5.82	20.00	232.50	1	8.50
Hylobatidae	<i>Hylobates</i>	<i>hoolock</i>	YES	41.00	6.88	23.33	NA	1	7.00
Hylobatidae	<i>Hylobates</i>	<i>klossii</i>	YES	37.00	5.92	11.00	210.00	1	NA
Hylobatidae	<i>Hylobates</i>	<i>lar</i>	YES	56.00	5.24	24.33	205.00	1	9.00
Hylobatidae	<i>Hylobates</i>	<i>muelleri</i>	YES	60.00	5.35	NA	207.00	1	NA
Hylobatidae	<i>Hylobates</i>	<i>pileatus</i>	YES	38.00	5.44	NA	228.00	1	NA
Hylobatidae	<i>Symphalangus</i>	<i>syndactylus</i>	YES	25.00	11.20	21.40	219.00	1	6.00
Panidae	<i>Pan</i>	<i>paniscus</i>	YES	59.40	36.85	48.00	230.00	1	9.83
Pongidae	<i>Pongo</i>	<i>pygmaeus</i>	YES	59.00	37.04	42.00	245.00	1	9.50
Aotidae	<i>Aotus</i>	<i>trivirgatus</i>	NO	22.10	0.74	5.88	137.00	1	3.00
Atelidae	<i>Alouatta</i>	<i>pigra</i>	YES	7.00	NA	NA	187.00	1	NA
Atelidae	<i>Alouatta</i>	<i>seniculus</i>	YES	25.00	5.21	12.40	190.00	1	4.04
Atelidae	<i>Ateles</i>	<i>belzebuth</i>	YES	37.00	7.65	NA	184.00	1	4.00
Atelidae	<i>Ateles</i>	<i>fusciceps</i>	YES	46.00	9.10	12.00	226.00	1	4.15
Atelidae	<i>Ateles</i>	<i>geoffroyi</i>	YES	47.10	7.29	2.25	232.00	1	5.00
Atelidae	<i>Brachyteles</i>	<i>arachnoides</i>	YES	40.00	8.07	24.00	232.50	1	7.50
Atelidae	<i>Lagothrix</i>	<i>lagothricha</i>	YES	32.00	7.07	20.04	225.00	1	8.17
Cebidae	<i>Cebus</i>	<i>albifrons</i>	YES	40.40	2.13	9.00	180.00	1	4.00
Cebidae	<i>Cebus</i>	<i>apella</i>	YES	46.00	2.52	13.68	158.00	1.5	4.67

Appendix C Life history and body size variables for the primate sample, raw data, continued*

Family	Genus	Species	PM before M3	Max Lifespan	Body Mass (F, kg)	Age at Weaning (mos)	Gestation (days)	Litter size	Age at Sexual Maturity (F, yrs)
Cebidae	<i>Cebus</i>	<i>capucinus</i>	YES	54.00	2.54	17.37	162.00	1	4.12
Cebidae	<i>Cebus</i>	<i>olivaceus</i>	YES	47.00	2.55	24.67	162.00	1	6.00
Pitheciidae	<i>Cacajao</i>	<i>calvus</i>	YES	35.80	2.88	18.00	182.00	1	3.00
Pitheciidae	<i>Callicebus</i>	<i>donacophius</i>	YES	25.00	1.21	4.56	165.00	1	NA
Pitheciidae	<i>Chiropotes</i>	<i>satanas</i>	YES	19.60	2.58	NA	150.00	1	4.00
Pitheciidae	<i>Pithecia</i>	<i>monachus</i>	NO	25.00	1.58	3.60	169.50	1	2.17
Galagidae	<i>Otolemur</i>	<i>crassicaudatus</i>	NO	22.70	1.10	4.60	130.00	1.5	1.36
Indriidae	<i>Avahi</i>	<i>sp.</i>	YES	NA	1.05	4.92	NA	1	NA
Indriidae	<i>Propithecus</i>	<i>diadema</i>	YES	21.00	6.26	6.00	135.50	1	3.25
Lemuridae	<i>Eulemur</i>	<i>fulvus</i>	NO	33.50	2.15	4.50	135.00	1.1	0.83
Lemuridae	<i>Lemur</i>	<i>catta</i>	YES	37.30	2.21	5.00	136.00	1.2	1.63
Lemuridae	<i>Lemur</i>	<i>mongoz</i>	NO	36.20	2.50	4.50	128.00	1.1	2.18
Lemuridae	<i>Varecia</i>	<i>variegata</i>	NO	37.00	3.00	4.50	102.20	2	1.67
Lepilemuridae	<i>Lepilemur</i>	<i>mustelinus</i>	NO	12.00	0.78	3.96	135.00	1	1.50
Loridae	<i>Loris</i>	<i>tardigradus</i>	NO	19.30	0.18	6.17	170.50	1.3	1.04
Loridae	<i>Nycticebus</i>	<i>bengalensis</i>	NO	25.80	1.50	6.00	187.00	1	1.25
Loridae	<i>Perodicticus</i>	<i>potto</i>	NO	26.80	1.10	5.00	197.00	1	1.50
Tarsiidae	<i>Tarsius</i>	<i>bancanus</i>	NO	16.30	0.12	2.64	178.00	1	2.52

Appendix C Life history and body size variables for the primate sample, raw data, continued*

Family	Genus	Species	PM before M3	Body Length (cm)	Age at M₁ eruption (yrs)	Brain Mass (F, g)	Estrous Cycle (days)	Interbirth Interval (mos)
Cercopithecidae	<i>Allenopithecus</i>	<i>nigroviridis</i>	YES	45.50	NA	62.50	NA	NA
Cercopithecidae	<i>Cercocebus</i>	<i>agilis</i>	YES	63.50	NA	114.70	30.00	16.60
Cercopithecidae	<i>Cercocebus</i>	<i>torquatus</i>	YES	NA	NA	86.00	33.00	13.00
Cercopithecidae	<i>Cercopithecus</i>	<i>aethiops</i>	YES	51.25	0.84	59.80	30.00	12.00
Cercopithecidae	<i>Colobus</i>	<i>angolensis</i>	YES	58.50	NA	73.50	NA	20.00
Cercopithecidae	<i>Colobus</i>	<i>guereza</i>	YES	NA	NA	82.30	NA	12.00
Cercopithecidae	<i>Colobus</i>	<i>polykomos</i>	YES	NA	NA	76.70	NA	14.73
Cercopithecidae	<i>Colobus</i>	<i>satanas</i>	YES	NA	NA	80.20	NA	16.00
Cercopithecidae	<i>Colobus</i>	<i>vellerosus</i>	YES	NA	NA	NA	NA	NA
Cercopithecidae	<i>Erythrocebus</i>	<i>patas</i>	YES	73.75	NA	106.60	33.00	12.80
Cercopithecidae	<i>Lophocebus</i>	<i>albigena</i>	YES	56.00	NA	NA	NA	19.47
Cercopithecidae	<i>Macaca</i>	<i>mulatta</i>	YES	56.55	1.32	81.30	28.00	20.63
Cercopithecidae	<i>Miopithecus</i>	<i>talapoin</i>	YES	38.50	NA	37.70	35.00	12.00
Cercopithecidae	<i>Nasalis</i>	<i>larvatus</i>	YES	64.75	NA	94.20	NA	18.00
Cercopithecidae	<i>Papio</i>	<i>hamadryas</i>	YES	68.60	1.71	145.50	30.00	15.00
Cercopithecidae	<i>Ptilocolobus</i>	<i>badius</i>	YES	NA	NA	NA	NA	NA
Cercopithecidae	<i>Procolobus</i>	<i>verus</i>	YES	46.00	NA	NA	NA	NA
Cercopithecidae	<i>Pygathrix</i>	<i>nemaus</i>	YES	68.60	NA	108.50	29.00	16.50
Cercopithecidae	<i>Semnopithecus</i>	<i>entellus</i>	NO	59.50	NA	98.20	24.00	19.50
Cercopithecidae	<i>Trachypithecus</i>	<i>cristatus</i>	YES	58.00	NA	NA	21.00	24.00
Cercopithecidae	<i>Trachypithecus</i>	<i>phayrei</i>	YES	NA	NA	67.60	NA	15.20

Appendix C Life history and body size variables for the primate sample, raw data, continued*

Family	Genus	Species	PM before M3	Body Length (cm)	Age at M₁ eruption (yrs)	Brain Mass (F, g)	Estrous cycle (days)	Interbirth Interval (mos)
Gorillidae	<i>Gorilla</i>	<i>gorilla</i>	YES	150.00	3.50	451.00	27.50	4.00
Hominae	<i>Homo</i>	<i>sapiens</i>	YES	16.75	6.33	NA	30.00	48.00
Hyllobatidae	<i>Hyllobates</i>	<i>agilis</i>	YES	53.75	NA	110.00	29.00	2.50
Hyllobatidae	<i>Hyllobates</i>	<i>hooleck</i>	YES	NA	NA	108.50	28.00	36.00
Hyllobatidae	<i>Hyllobates</i>	<i>klossii</i>	YES	NA	NA	91.10	NA	NA
Hyllobatidae	<i>Hyllobates</i>	<i>lar</i>	YES	NA	1.75	107.70	27.00	32.97
Hyllobatidae	<i>Hyllobates</i>	<i>muelleri</i>	YES	NA	NA	NA	NA	2.96
Hyllobatidae	<i>Hyllobates</i>	<i>pileatus</i>	YES	NA	NA	NA	NA	NA
Hyllobatidae	<i>Symphalangus</i>	<i>syndactylus</i>	YES	NA	1.75	110.90	NA	20.23
Panidae	<i>Pan</i>	<i>paniscus</i>	YES	78.75	3.33	376.00	36.00	54.00
Pongidae	<i>Pongo</i>	<i>pygmaeus</i>	YES	137.50	3.50	330.30	28.00	42.00
Aotidae	<i>Aotus</i>	<i>trivirgatus</i>	NO	30.50	0.36	18.20	16.00	12.70
Atelidae	<i>Alouatta</i>	<i>pigra</i>	YES	NA	NA	NA	NA	NA
Atelidae	<i>Alouatta</i>	<i>seniculus</i>	YES	NA	NA	57.90	NA	17.00
Atelidae	<i>Ateles</i>	<i>belzebuth</i>	YES	NA	NA	106.60	NA	25.33
Atelidae	<i>Ateles</i>	<i>fusciceps</i>	YES	NA	NA	114.70	NA	36.50
Atelidae	<i>Ateles</i>	<i>geoffroyi</i>	YES	NA	NA	110.90	NA	32.33
Atelidae	<i>Brachyteles</i>	<i>arachnoides</i>	YES	54.50	NA	120.40	30.00	36.00
Atelidae	<i>Lagothrix</i>	<i>lagothricha</i>	YES	59.70	NA	96.40	30.50	24.00
Cebidae	<i>Cebus</i>	<i>albifrons</i>	YES	43.50	1.06	82.00	18.00	14.33
Cebidae	<i>Cebus</i>	<i>apella</i>	YES	NA	1.28	71.00	NA	22.37

Appendix C Life history and body size variables for the primate sample, raw data, continued*

Family	Genus	Species	PM before M3	Body Length (cm)	Age at M₁ eruption (yrs)	Brain Mass (F, g)	Estrous cycle (days)	Interbirth Interval (mos)
Cebidae	<i>Cebus</i>	<i>capucinus</i>	YES	NA	NA	NA	NA	26.77
Cebidae	<i>Cebus</i>	<i>olivaceus</i>	YES	NA	NA	NA	NA	26.40
Pitheciidae	<i>Cacajao</i>	<i>calvus</i>	YES	43.50	NA	73.30	16.00	24.00
Pitheciidae	<i>Callicebus</i>	<i>donacophius</i>	YES	34.50	NA	22.40	NA	12.00
Pitheciidae	<i>Chiropotes</i>	<i>satanas</i>	YES	41.90	NA	NA	NA	NA
Pitheciidae	<i>Pithecia</i>	<i>monachus</i>	NO	50.25	NA	31.70	18.00	NA
Galagidae	<i>Otolemur</i>	<i>crassicaudatus</i>	NO	33.50	NA	NA	NA	3.97
Indridae	<i>Avahi</i>	<i>sp.</i>	YES	37.50	0.08	10.00	NA	NA
Indridae	<i>Propithecus</i>	<i>diadema</i>	YES	50.00	0.29	26.80	NA	24.83
Lemuridae	<i>Eulemur</i>	<i>fulvus</i>	NO	44.00	0.42	NA	30.00	17.90
Lemuridae	<i>Lemur</i>	<i>catta</i>	YES	42.00	0.34	23.50	40.00	17.03
Lemuridae	<i>Lemur</i>	<i>mongoz</i>	NO	35.00	NA	NA	NA	12.00
Lemuridae	<i>Varecia</i>	<i>variegata</i>	NO	53.50	0.48	31.20	30.00	NA
Lepilemuridae	<i>Lepilemur</i>	<i>mustelinus</i>	NO	32.50	0.13	9.50	NA	21.00
Loridae	<i>Loris</i>	<i>tardigradus</i>	NO	NA	NA	NA	NA	9.60
Loridae	<i>Nycticebus</i>	<i>bengalensis</i>	NO	32.00	NA	NA	NA	NA
Loridae	<i>Perodicticus</i>	<i>potto</i>	NO	34.75	NA	NA	NA	6.60
Tarsiidae	<i>Tarsius</i>	<i>bancanus</i>	NO	12.25	0.05	3.80	22.50	9.00

*PM is premolars, M3 is third molar, F is female, g is grams, mos is months, yrs is years. References for the life history and body size variables are: Harvey and Cluttonbrock 1985, Smith 1994, Smith and Jungers 1997, Jungers et al. 1998, Nowak 1999, Carey and Judge 2000, Roycewicz 2001, Martin 2004, Schwartz et al. 2005, McCann 2009, Guthrie and Frost 2011, McGinness 2011, Smith 2015

Appendix D Life history and body size variables for the artiodactyls, raw data*

Family	Genus	Species	P4 erupts after M3	Max lifespan (yr)	Height (cm)	Body Length (cm)	Body mass (kg)	Litter Size
Bovidae	<i>Hippotragus</i>	<i>equinus</i>	YES	25.9	130.0	222.5	245.0	1
Bovidae	<i>Hippotragus</i>	<i>niger</i>	YES	22.2	130.0	222.5	245.0	1
Bovidae	<i>Alcelaphus</i>	<i>busei</i>	YES	22.5	NA	197.5	137.5	1
Bovidae	<i>Alcelaphus</i>	<i>lichtensteini</i>	YES	NA	127.5	180.0	162.5	1
Bovidae	<i>Connochaetes</i>	<i>taurinus</i>	YES	24.3	105.0	195.0	145.0	1
Bovidae	<i>Naemohedus</i>	<i>griseus</i>	YES	19.0	89.5	160.0	95.0	1
Bovidae	<i>Ovibos</i>	<i>moschatus</i>	YES	27.4	135.0	NA	380.0	1
Bovidae	<i>Budorcas</i>	<i>taxicolor</i>	YES	21.9	104.0	167.5	275.0	1
Bovidae	<i>Rupicapra</i>	<i>pyrenaica</i>	YES	20.7	78.5	110.0	37.0	1
Bovidae	<i>Rupicapra</i>	<i>rupicapra</i>	YES	17.6	78.5	110.0	37.0	1
Bovidae	<i>Capra</i>	<i>hircus</i>	NO	20.8	110.0	171.0	130.0	1
Bovidae	<i>Capra</i>	<i>caucasica</i>	NO	19.3	110.0	171.0	130.0	1
Bovidae	<i>Hemitragus</i>	<i>jemlahicus</i>	NO	21.8	62.0	NA	23.0	1
Bovidae	<i>Pseudois</i>	<i>nayaur</i>	YES	20.9	NA	130.0	67.5	1
Bovidae	<i>Ovis</i>	<i>canadensis</i>	NO	20.6	NA	174.0	84.5	1
Bovidae	<i>Ovis</i>	<i>aries</i>	NO	22.8	NA	174.0	84.5	1
Bovidae	<i>Hemitragus</i>	<i>hylocrius</i>	NO	17.3	62.0	NA	23.0	1
Bovidae	<i>Oreotragus</i>	<i>oreotragus</i>	YES	25.9	52.5	91.0	12.5	1
Bovidae	<i>Kobus</i>	<i>ellipsiprymnus</i>	YES	30.0	115.0	200.0	262.5	1
Bovidae	<i>Redunca</i>	<i>fulvovirgata</i>	YES	15.0	85.0	140.0	147.5	1
Bovidae	<i>Redunca</i>	<i>redunca</i>	YES	NA	85.0	140.0	147.5	1
Bovidae	<i>Madoqua</i>	<i>guentheri</i>	YES	17.5	40.0	66.0	4.6	1
Bovidae	<i>Madoqua</i>	<i>kirkii</i>	YES	17.3	40.0	66.0	4.6	1

Appendix D Life history and body size variables for the artiodactyls, raw data, continued*

Family	Genus	Species	P4 erupts after M3	Max lifespan (yr)	Height (cm)	Body Length (cm)	Body mass (kg)	Litter Size
Bovidae	<i>Gazella</i>	<i>bennettii</i>	YES	NA	60.0	100.0	16.0	1
Bovidae	<i>Gazella</i>	<i>dorcas</i>	YES	23.7	60.0	100.0	16.0	1
Bovidae	<i>Antidorcas</i>	<i>marsupialis</i>	YES	19.8	80.0	130.0	38.5	1
Bovidae	<i>Litocranius</i>	<i>walleri</i>	YES	17.3	95.0	150.0	43.5	1
Bovidae	<i>Raphicerus</i>	<i>campestris</i>	YES	9.3	52.5	80.0	11.5	1
Bovidae	<i>Cephalophus</i>	<i>weynsi</i>	YES	15.2	47.5	85.0	17.5	1
Bovidae	<i>Aepyceros</i>	<i>melampus</i>	YES	25.6	85.0	140.0	60.0	1
Bovidae	<i>Neotragus</i>	<i>moschatus</i>	YES	13.5	24.0	52.5	7.0	1
Bovidae	<i>Bubalus</i>	<i>bubalis</i>	YES	34.9	169.5	275.0	950.0	1
Bovidae	<i>Syncerus</i>	<i>caffer</i>	YES	32.8	157.0	255.0	700.0	1
Bovidae	<i>Bison</i>	<i>bison</i>	YES	33.5	167.5	280.0	725.5	1
Bovidae	<i>Bos</i>	<i>grunniens</i>	YES	26.3	182.5	282.5	850.0	1
Bovidae	<i>Tragelaphus</i>	<i>scriptus</i>	YES	15.3	22.5	50.0	2.0	1
Moschidae	<i>Moschus</i>	<i>berezovskii</i>	YES	27.5	52.0	93.0	12.5	1.5
Cervidae	<i>Hydropotes</i>	<i>inermis</i>	YES	13.9	52.5	NA	15.0	1
Cervidae	<i>Rangifer</i>	<i>tarandus</i>	YES	21.8	117.5	187.5	151.0	1
Cervidae	<i>Hippocamelus</i>	<i>antisensis</i>	YES	10.6	84.0	152.5	55.0	1
Cervidae	<i>Ozotoceros</i>	<i>bezoarticus</i>	YES	21.9	72.5	125.0	35.0	1
Cervidae	<i>Pudu</i>	<i>puda</i>	YES	18.3	40.0	85.0	12.0	1
Cervidae	<i>Odocoileus</i>	<i>hemionus</i>	YES	22.0	97.5	177.5	100.0	1
Cervidae	<i>Mazama</i>	<i>americana</i>	YES	17.1	55.0	103.5	20.0	1
Cervidae	<i>Cervus</i>	<i>elaphus</i>	YES	31.5	135.0	202.5	200.0	1
Cervidae	<i>Elaphodus</i>	<i>cephalophus</i>	YES	22.7	60.0	135.0	33.5	1

Appendix D Life history and body size variables for the artiodactyls, raw data, continued*

Family	Genus	Species	P4 erupts after M3	Max lifespan (yr)	Height (cm)	Body Length (cm)	Body mass (kg)	Litter Size
Cervidae	<i>Muntiacus</i>	<i>muntjak</i>	YES	18.8	52.5	112.0	25.0	1
Cervidae	<i>Muntiacus</i>	<i>reevesi</i>	YES	23.2	52.5	112.0	25.0	1
Antilocapridae	<i>Antilocapra</i>	<i>americana</i>	YES	15.5	88.5	140.0	50.0	2
Hippopotamidae	<i>Hippopotamus</i>	<i>amphibius</i>	NO	61.2	144.5	270.0	1800.0	1
Camelidae	<i>Lama glama</i>	<i>glama</i>	NO	28.9	115.0	NA	130.0	1
Suidae	<i>Babyrussa</i>	<i>babyrussa</i>	NO	22.9	72.5	93.5	80.0	1.5
Suidae	<i>Sus</i>	<i>scrofa</i>	NO	27.0	82.5	NA	192.5	5
Suidae	<i>Potamochoerus</i>	<i>porcus</i>	NO	22.0	76.0	125.0	70.0	3.5
Suidae	<i>Phacochoerus</i>	<i>aethiopicus</i>	NO	20.9	74.5	167.5	82.0	3
Suidae	<i>Hylochoerus</i>	<i>meinertzhageni</i>	NO	NA	93.0	170.0	230.0	3
Tayassuidae	<i>Catagonus</i>	<i>wagneri</i>	NO	NA	NA	NA	36.5	2.5
Tayassuidae	<i>Pecari</i>	<i>tajacu</i>	NO	31.5	NA	NA	26.5	2
Tayassuidae	<i>Tayassu</i>	<i>pecari</i>	NO	28.5	NA	NA	32.5	2

* P4 is fourth premolar, M3 is third molar, yr is years, cm is centimeters, kg is kilograms. Lifespan for *Moschus* was taken from captive individuals (Green 1987). References for life history and body size variables are: Grzimek 1990, Tacutu et al. 2013. Appendix modified from Monson and Hlusko 2016