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RESEARCH ARTICLE

Breaking the rules: Phylogeny, not life history, explains dental eruption sequence in primates

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Abstract

Objectives: Although a great deal is known about the biology of tooth development and eruption, there remains disagreement about the factors driving the evolution of dental eruption sequence. We assessed postcanine eruption sequence across a large sample of primates to test two hypotheses: (1) Dental eruption sequence is significantly correlated with life history and body size variables that capture postnatal growth and longevity (Schultz's rule), and (2) Dental eruption sequence is conserved phylogenetically.

Materials and methods: We assessed postcanine dental eruption sequence for 194 individuals representing 21 primate genera spanning eight families. With the inclusion of an additional 29 primate genera from the literature, this is the most comprehensive report on dental eruption sequence in primates to date. We used a series of phylogenetic analyses to statistically compare dental eruption sequence to life history and body size and test for phylogenetic signal in these traits.

Results: Dental eruption sequence is conserved phylogenetically in primates, and body and brain size are both significantly associated with dental eruption sequence. Ancestral state reconstruction supports the hypothesis that the third molar erupted before one or more of the premolars in the ancestor of primates, and derived clades within primates evolved an eruption sequence in which the third molar erupts after the premolars.

Discussion: Schultz's rule, as it is currently written and applied, is not supported by this extended data set. Our results demonstrate that dental eruption sequence is a far better predictor of phylogeny and will likely prove useful in phylogenetic hypotheses about relationships between extinct and extant mammalian taxa. The evolution of dental eruption sequence is likely driven by factors that significantly influence body size and mandibular symphyseal fusion.

KEYWORDS

ancestral state reconstruction, body size, mandibular symphyseal fusion, Schultz's rule

1 | INTRODUCTION

Almost all terrestrial mammals are diphyodont with two generations of teeth: deciduous and permanent. Having multiple generations of teeth allows for size and complexity to increase while the individual develops from juvenile to adult, matching changes in overall body size and shape (Hillson, 2005). The timing of tooth eruption is highly correlated between teeth 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 such as life history, the timing of

permanent tooth development, the size of the face and dental arch, juvenile and adult diets, and even group dynamics such as intrasex competition (e.g., Bryant, 1990; Leigh, Setchell, Charpentier, Knapp, and Wickings, 2008; Schultz, 1935, 1956; Smith, 1994, 2000).

Tooth eruption has been well-studied in mammals, and a great deal is known about the cellular and molecular processes associated with eruption (e.g., Cahill, 1969; Cahill, Marks, Wise, & Gorski, 1988; Marks, 1973; Wise, Frazier-Bowers, and D'Souza, 2002). However, less is known about the factors driving the timing and sequence of eruption (e.g., Kjær, 2014; Smith et al., 2015; Woodroffe et al., 2010). 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 (Bryant, 1990; Leigh et al., 2008; Schultz, 1935, 1950, 1956; Smith, 1994, 2000; Smith, Crummett, and Brandt, 1994; Suri, Gagari, and Vastardis, 2004; Wise et al., 2002). There has also been considerable interest in the dental eruption sequence of fossil mammals, including primates (e.g., Gregory, 1920; Kay and Simons, 1983; Lamberton, 1938; Wallace, 1977), whales (Kellogg, 1936), and other extinct groups (e.g., Cifelli 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 such as longevity and postnatal growth (Schultz, 1956, 1960; Smith, 1994, 2000), and (2) Dental eruption sequence is a good reflection of phylogeny in primates, and likely other mammals (Byrd, 1981; Schwartz, 1974; Tattersall and Schwartz, 1974).

1.1 | Schultz's rule

Schultz's (1935, 1956, 1960) proposal that dental eruption sequence is an adaptation to rates of postnatal growth has been cited hundreds of times. What has come to be known as "Schultz's rule" states that replacement non-molar teeth erupt earlier relative to the molars in long-lived species with a slower rate of growth; that is, those with a slower life history. Smith (2000) tested Schultz's rule in primates and ungulates, comparing dental eruption sequence and a measure of growth speed, assessed as age at emergence of the first molar. Smith (2000) reported 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 I_1 or P_3 relative to the mandibular molars). Overall, Smith (2000) suggested that ungulates tend to follow Schultz's rule, and primates 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., Franzen et al., 2009; Robson and Wood, 2008; Schwartz et al., 2005), as well as other mammals (e.g., Asher and Olbricht, 2009; Billet and Martin, 2011; Dirks, Anemone, Holroyd, Reid, and Walton, 2009; Loe, Meisingset, Mysterud, Langvatn, & Stenseth, 2004; Macho and Williamson, 2002; McGee and Turnbull, 2010; Townsend and Croft, 2010; Yamanaka, Yasui, Sonomura, Iwai, & Uemura, 2010), 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 postnatal growth (e.g., Hellmund, 2016; Jordana et al., 2013).

As a counterpoint to Schultz's hypothesis that dental eruption sequence is related to life history and rates of postnatal growth, several researchers have argued that dental eruption sequence, whether or not it is correlated with other factors, has conserved phylogenetic signal (Byrd, 1981; Schwartz, 1974; Tattersall and Schwartz, 1974;

Veitschegger and Sánchez-Villagra, 2016). Additionally, Schultz's rule has been challenged by authors studying groups of primates (Godfrey, Samonds, Wright, and King, 2005; Guthrie and Frost, 2011; Jogahara and Natori, 2012; King, Godfrey, and Simons, 2001; Schwartz et al., 2005), and other mammals (Monson and Hlusko, 2016; Veitschegger and Sánchez-Villagra, 2016).

This history of research demonstrates significant disagreement on whether life history variables, phylogeny, or possibly other factors, are driving the evolution of dental eruption sequence. To expand on previous studies and to test Schultz's rule in primates more fully, we collected dental eruption sequence for 21 genera of extant primate, supplemented by data on 29 additional genera from the literature, thereby making this the most comprehensive examination of primate dental eruption sequence to date. We test two hypotheses: (H1) Dental eruption sequence is significantly correlated with life history and body size variables that capture postnatal growth and longevity irrespective of phylogenetic proximity (Schultz's rule), and (H2) Dental eruption sequence is conserved phylogenetically, such that eruption sequences are more similar in more closely related species regardless of life history and body size variables.

2 | MATERIALS AND METHODS

To add to the literature, we assessed postcanine dental eruption sequence in a sample of 21 primate genera and 46 primate species (n = 194), all examined by TM, to thoroughly sample dental eruption sequence in primates beyond what has been described in the literature. All specimens are held in the Smithsonian National Museum of Natural History (NMNH) in Washington, D.C. (Table 1).

Because so much work has already been done to compile dental eruption sequences, we focused on species and genera that are less well-represented in the literature. We relied on published data for species such as *Homo sapiens*, *Papio hamadryas*, and *Macaca mulatta*. We 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*, we examined every cranial specimen of the focal species available at the NMNH. Our effective sample size is derived from the examination of n = 4,031 specimens, of which ~4.7% were at the appropriate ontogenetic stage to assess dental eruption sequence. We emphasize the large primate collection sizes needed to conduct the taxonomically broad investigation of primate dental eruption sequence necessary for phylogenetic analyses, and we present a breakdown of the full sample examined by genus and species in the Supporting Information (Appendices A,B) to aid future researchers wishing to examine postcanine dental eruption sequence in the Smithsonian primate collections.

Additionally, we collected data on dental eruption sequence for 29 primate 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, we collected data on six fossil species from the literature: extinct lemurs *Archaeolemur* (two species) and *Hadropithecus stenognathus*, fossil strepsirrhine *Megaladapis*,

TABLE 1 Specimen numbers of the primates and primate-outgroups used to assess dental eruption sequence

Family	Genus	Species	Sample size (n)	Specimen numbers[a]
(Catarrhini)				
Cercopithecidae	*Allenopithecus*	*nigroviridis*	1	NMNH 300808
	Cercocebus	*agilis*	1	NMNH 537772
		torquatus	11	NMNH 220370, NMNH 220351, NMNH 220350, NMNH 220372, NMNH 220353, NMNH 220352, NMNH 218842, NMNH 598495, NMNH 270593, NMNH 49720, NMNH 271011
	Cercopithecus	*aethiops*	NA	literature
	Colobus	*angolensis*	1	NMNH 237325
		guereza	4	NMNH 163226, NMNH 163263, NMNH 464983, NMNH 522951
		polykomos	1	NMNH 481788
		satanas	1	NMNH 598561
		vellerosus	1	NMNH 477322
	Erythrocebus	*patas*	3	NMNH 410530, NMNH 410529, NMNH 538311
	Lophocebus	*albigena*	2	NMNH 452499, NMNH 220089
	Macaca	*mulatta*	NA	literature
	Miopithecus	*ogouensis*	3	NMNH 598531, NMNH 220349, NMNH 396195
	Nasalis	*larvatus*	NA	literature
	Papio	*hamadryas*	NA	literature
	Piliocolobus	*badius*	3	NMNH 381458, NMNH 481794, NMNH 83908
	Presbytis	*frontata*	1	NMNH 199188
		hosei	6	NMNH 198283, NMNH 198280, NMNH 198285, NMNH 198291, NMNH 198290, NMNH 292560
		melalophos	3	NMNH 115503, NMNH 86897, NMNH 83408
		potenziani	2	NMNH 121664, NMNH 252314
	Procolobus	*verus*	NA	literature
	Pygathrix	*nemaeus*	1	NMNH 356854
	Semnopithecus	*entellus*	NA	literature
	Trachypithecus	*cristatus*	2	NMNH 156311, NMNH 257685
		phayrei	1	NMNH 303035
Gorillidae	*Gorilla*	*gorilla*	NA	literature
Hominidae	*Homo*	*sapiens*	NA	literature
Hylobatidae	*Hylobates*	*agilis*	2	NMNH 113177, NMNH 143576
		hoolock	1	NMNH 279146
		klossii	2	NMNH 121681, NMNH 121677
		lar	4	NMNH 111990, NMNH 307763, NMNH 112574, NMNH 083264
		muelleri	4	NMNH 198271, NMNH 198842, NMNH 198268, NMNH 196779
		pileatus	2	NMNH 321550, NMNH 347648
		sp.	2	NMNH 300923, NMNH 395693
	Symphalangus	*syndactylus*	2	NMNH 141163, NMNH 395691
Panidae	*Pan*	*paniscus*	NA	literature
Pongidae	*Pongo*	*pygmaeus*	NA	literature
		Total	**67**	
(Platyrrhini)				
Aotidae	*Aotus*	*trivirgatus*	NA	literature
Atelidae	*Alouatta*	*palliata*	14	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, NMNH A22833
		pigra	2	NMNH 292201, NMNH 292182
		seniculus	12	

TABLE 1 (Continued)

Family	Genus	Species	Sample size (n)	Specimen numbers[a]
				NMNH 194351, NMNH 261320, NMNH 44382, NMNH 443747, NMNH 443376, NMNH 372757, NMNH 143148, NMNH 281673, NMNH 281756, NMNH 281758, NMNH 194351, NMNH 261320
	Ateles	*ater* (sp.)	6	NMNH 63425, NMNH 82746, NMNH 59160, NMNH 397952, NMNH 49712, NMNH A984
		belzebuth	8	NMNH 281811, NMNH 281779, NMNH 281790, NMNH 281083, NMNH 281793, NMNH 281804, NMNH 443226, NMNH 406478
		chamek	1	NMNH 194338
		fusciceps	3	NMNH 362294, NMNH 521041, NMNH 336279
		geoffroyi	10	NMNH A14162, NMNH 315841, NMNH 74671, NMNH 282273, NMNH 292216, NMNH 292214, NMNH 292218, NMNH 284950, NMNH 337699, NMNH 337865
	Brachyteles	*arachnoides*	NA	literature
	Lagothrix	*lagotricha*	3	NMNH 282791, NMNH 398460, NMNH 399302
Callitrichidae	*Callimico*	*goeldii*	2	NMNH 399073, NMNH 464993
Cebidae	*Cebus*	*albifrons*	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
		apella	19	NMNH 518303, NMNH 518302, NMNH 547896, NMNH 397941, NMNH 397959, NMNH 240987, NMNH 518465, NMNH 518403, NMNH 518408, NMNH 518467, NMNH 518416, NMNH 518408, NMNH 518271, NMNH 518274, NMNH 518491, NMNH 518458, NMNH 518511, NMNH 518498, NMNH 518335
		capucinus	10	NMNH 291230, NMNH 25311, NMNH 284774, NMNH 283908, NMNH 283907, NMNH 306828, NMNH 310310, NMNH 283940, NMNH 223389, NMNH 14220
		libidinosus[b]	6	NMNH 518526, NMNH 518399, NMNH 518522, NMNH 518531, NMNH 518521, NMNH 518402
		olivaceus	6	NMNH 372768, NMNH 258501, NMNH 406635, NMNH 148742, NMNH 336197, NMNH 296286
	Saimiri	*sciureus*	7	NMNH 522059, NMNH 522058, NMNH 398685, NMNH 397802, NMNH 397817, NMNH 397816, NMNH 398628
Pitheciidae	*Cacajao*	*calvus*	NA	literature
	Callicebus	*donacophilus*	NA	literature
	Chiropotes	*satanas*	NA	literature
	Pithecia	*monachus*	1	NMNH 38498/16606
		Total	**123**	
(Strepsirrhini, Tarsiiformes, Adapiformes, Plesiadapiformes)				
Archaeolemuridae[c]	*Archaeolemur*[c]	sp. cf. *edwardsi*[c]	NA	literature
		majori[c]	NA	literature
	Hadropithecus[c]	*stenognathus*[c]	NA	literature
Galagidae	*Otolemur*	*crassicaudatus*	NA	literature
Indriidae	*Avahi*	sp.	NA	literature
	Propithecus	*diadema* (spp.)[d]	1	NMNH 63348
Lemuridae	*Eulemur*	*fulvus*	NA	literature
		mongoz[e]	NA	literature
	Lemur	*catta*	NA	literature
	Lepilemur	*mustelinus* (spp.)[f]	NA	literature
	Varecia	*variegata*	3	NMNH 84381, NMNH 84383, NMNH 503392

(Continues)

TABLE 1 (Continued)

Family	Genus	Species	Sample size (*n*)	Specimen numbers[a]
Lorisidae	*Loris*	*tardigradus*	NA	literature
	Nycticebus	*bengalensis*	NA	literature
	Perodicticus	*potto*	NA	literature
Megaladapidae[c]	*Megaladapis*[c]	sp.	NA	literature
Tarsiidae	*Tarsius*	*bancanus*	NA	literature
		spectrum	NA	literature
Adapidae[c]	*Adapis*[c]	*parisiensis*[c]	NA	literature
Plesiadapidae[c]	*Acidomomys*[c]	*hebeticus*[c]	NA	literature
		Total	**4**	
(Outgroups: Dermoptera, Scandentia)				
Cynocephalidae	*Galeopterus*	*variegatus*	8	NMNH 121854, NMNH 253411, NMNH 154600, NMNH 258871, NMNH 317119, NMNH 300827, NMNH 300826, NMNH 197203
Ptilocercidae	*Ptilocercus*	*lowii*	NA	literature
Tupaiidae	*Tupaia*	*glis*	NA	literature
		Total	**8**	
GRAND TOTAL			**202**	

[a] NMNH is National Museum of Natural History.
[b] NMNH catalogue lists this as hybrid species *apella nigritus + libidinosus*.
[c] Indicates an extinct taxon.
[d] Revised taxonomy has divided *Propithecus diadema* into multiple species (Groves and Helgen, 2007).
[e] *Eulemur mongoz* was previously published as *Lemur mongoz* (Schwartz, 1974; Tattersall and Schwartz, 1991).
[f] Revised taxonomy has divided *Lepilemur mustelinus* into multiple species (Rumpler and Albignac, 1978).

adapiforme *Adapis*, and plesiadapid *Acidomomys*. With the exception of *Archaeolemur*, *Eulemur*, and *Tarsius*, the dental eruption sequence for only one species from each genus was taken from the literature. While our compilation of the published literature is not exhaustive, it is broad enough to provide important perspective on the evolution of dental eruption sequence. Some aspects of primate taxonomy have changed over the last 40 years, and species with updated names or taxonomic designation are noted in table footnotes. As with all studies using data from published sources, we rely on the accuracy and precision of the methods reported. All methods reported are comparable to our methods for assessing dental eruption sequence. However, there is always the possibility of interindividual error associated with using other researchers' data, and we acknowledge that possibility here. A list of references for the dental eruption sequences from the literature is available in Table 2.

2.1 | Data collection methods

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, Sage, and Mahaney, 2011). With this in mind, we restricted our study to the functional grinding teeth in primates, the postcanine dentition, which consists of premolars and molars. We visually examined specimens across ontogenetic stages. Eruption sequence was defined as either having the third molar erupt after the premolars, or vice versa (Figure 1). In some primate species, there was significant variation in whether the third molar or one of the premolars erupts last. Such species were categorized as variable (Figure 2). We examined eruption sequence in both the maxilla and mandible of each specimen where available. While we found no difference in eruption sequence between maxilla and mandible in the majority of cases, we did note several examples of intra- and interspecific variation in eruption sequence (Figure 2), and that eruption of the permanent teeth tends to occur earlier in the mandible than in their maxillary isomeres.

2.2 | Test of intraspecific variation

We looked at every specimen available for almost all primate genera held at the National Museum of Natural History (*n* = 4,031) in our effort to assess the level of intraspecific variation in dental eruption sequence in primates. Of this sample, *n* = 194 are at the appropriate ontogenetic stage to assess dental eruption sequence. On the basis of this examination, we identified two general categories of primate postcanine dental eruption sequence. The first includes taxa that show a consistent dental eruption sequence in which either one of the premolars or the third molar is the last of the postcanine dentition to erupt. The other category includes taxa in which intraspecific variation in dental eruption sequence occurs with such regularity that it can be considered a phenotype. In every taxon classified as exhibiting intraspecific variation in dental eruption sequence in this study, more than 30% of the specimens examined exhibited a nondominant dental eruption sequence and/or intraindividual dental eruption sequence. The significance of this intraspecific variability is still not yet understood and deserves greater study. It also raises into question dental eruption sequences reported for single specimens, particularly in the

TABLE 2 References for the dental eruption sequences from the literature

Clade	Family	Genus	Species	Reference
Catarrhini	Cercopithecidae	*Cercopithecus*	*aethiops*	Swindler 2002
		Macaca	*mulatta*	Schwartz et al. 2005
		Nasalis	*larvatus*	Harvati 2000
		Papio	*hamadryas*	Schwartz et al. 2005
		Procolobus	*verus*	Swindler 2002
		Semnopithecus	*entellus*	Schwartz et al. 2005
	Gorillidae	*Gorilla*	*gorilla*	Schwartz et al. 2005
	Hominidae	*Homo*	*sapiens*	Schwartz et al. 2005
	Panidae	*Pan*	*paniscus*	Schwartz et al. 2005
	Pongidae	*Pongo*	*pygmaeus*	Schwartz et al. 2005
Platyrrhini	Aotidae	*Aotus*	*trivirgatus*	Schwartz et al. 2005
	Atelidae	*Brachyteles*	*arachnoides*	Henderson 2007
	Pitheciidae	*Cacajao*	*calvus*	Henderson 2007
		Callicebus	*donacophilus*	Henderson 2007
		Chiropotes	*satanas*	Henderson 2007
Strepsirrhini	Archaeolemuridae[a]	*Archaeolemur*[a]	sp. cf. *edwardsi*[a]	Schwartz et al. 2005
			majori[a]	Schwartz et al. 2005
		Hadropithecus[a]	*stenognathus*[a]	Schwartz et al. 2005
	Galagidae	*Otolemur*	*crassicaudatus*	Schwartz 1974
	Indriidae	*Avahi*	sp.	Godfrey et al. 2005
	Lemuridae	*Eulemur*	*fulvus*	Schwartz et al. 2005
			mongoz[b]	Schwartz 1974
		Lemur	*catta*	Schwartz 1974
		Lepilemur	*mustelinus* (spp.)[c]	Schwartz 1974
	Lorisidae	*Loris*	*tardigradus*	Schwartz 1974
		Nycticebus	*bengalensis*	Schwartz 1974
		Perodicticus	*potto*	Schwartz 1974
	Megaladapidae[a]	*Megaladapis*[a]	sp.	Schwartz et al. 2005
Tarsiiformes	Tarsiidae	*Tarsius*	*bancanus*	Guthrie and Frost 2011
			spectrum	Schwartz 1974
Adapiformes[a]	Adapidae[a]	*Adapis*[a]	*parisiensis*[a]	Smith 2000
Plesiadapiformes[a]	Plesiadapidae[a]	*Acidomomys*[a]	*hebeticus*[a]	Bloch et al. 2002
Outgroup: Scandentia	Ptilocercidae	*Ptilocercus*	*lowii*	Butler 1980, Dirks et al. 2010
	Tupaiidae	*Tupaia*	*glis*	Schwartz et al. 2005; Shigehara 1980

[a] Indicates an extinct taxon.
[b] *Eulemur mongoz* was previously published as *Lemur mongoz* (Schwartz, 1974; Tattersall and Schwartz, 1991).
[c] Revised taxonomy has divided *Lepilemur mustelinus* into multiple *Lepilemur* species (Rumpler and Albignac, 1978).

fossil record. We note that larger sample sizes may help clarify the extent of intraspecific variation in primate dental eruption sequence.

While a detailed study of intraspecific variation across taxa is beyond the scope of this investigation, we did conduct an initial investigation of intraspecific variation in eruption sequence by examining every specimen of *Cebus* at the NMNH (n = 849).

2.3 | Analytical methods

We generated a phylogeny of the primate sample using molecular data from six autosomal genes and 11 mitochondrial genes from the 10kTrees database (Arnold, Matthews, and Nunn, 2010). Some of the species included in this study are not available in the 10kTrees database, and these were added in manually via the Mesquite Program

v3.11 (Maddison and Maddison, 2016). *Tarsius spectrum*, *Presbytis frontata*, and *Presbytis hosei* were manually placed in the primate phylogeny using data from the published literature (Shekelle, Meier, Wahyu, and Ting, 2010; Vun, Mahani, Lakim, Ampeng, and Md-Zain, 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*. Species phylogeny within the genus *Ateles* is debated (e.g., Morales-Jimenez, Disotell, and Di Fiore, 2015), but all ateline species have the same postcanine dental eruption sequence in this study, so the exact distribution of species does not affect ancestral state reconstruction; consequently, *Ateles ater* was placed as a sister taxon to *Ateles belzebuth*.

We collected life history and body size data for the majority of primates included in this study in an effort to test for any relationship between life history and dental eruption sequence (Schultz's rule).
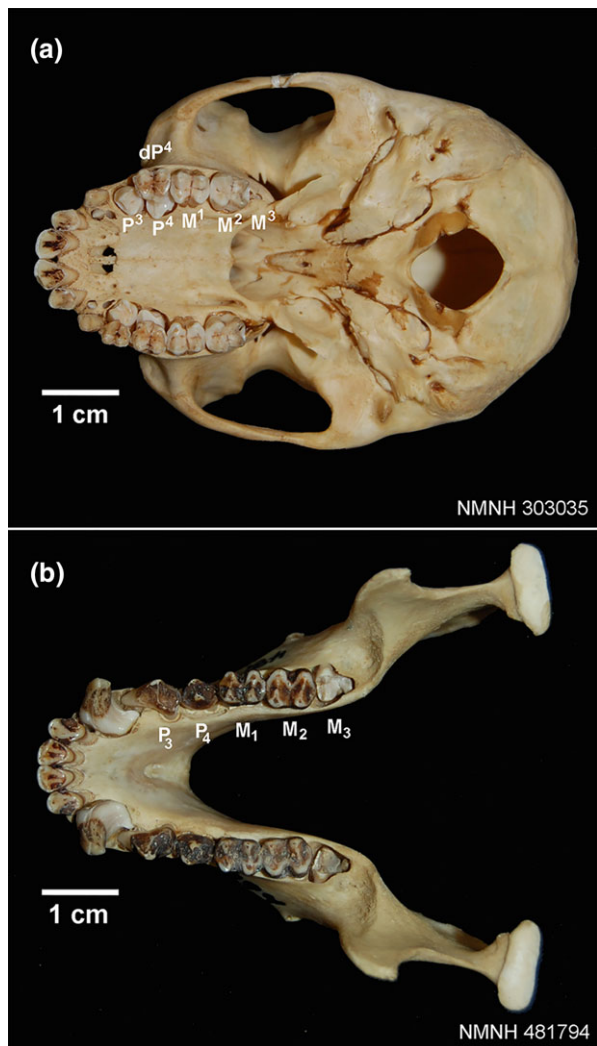
FIGURE 1 Examples of eruption sequence in primates. M is molar, P is premolar, d is deciduous, and the number denotes tooth number, for example, dP^4 is maxillary deciduous premolar 4, (a) Eruption of the M^3 last in *Trachypithecus phayrei*. Note that the M^3 is barely visible in the crypt while P^4 is well on the way to replacing dP^4, (b) Eruption of the M$_3$ last in *Piliocolobus badius*. Note that the M$_3$ has not yet fully erupted while the P$_4$ is erupted and in occlusion

FIGURE 2 Examples of variation in dental eruption sequence in *Alouatta*. M is molar, P is premolar, d is deciduous, and the number denotes tooth number, for example, dP$_4$ is mandibular deciduous premolar 4, (a) Eruption of the M^3 last in *A. pigra* (palatal view). Note that the M^3 is in the crypt while the premolars are fully erupted and in occlusion, (b) Eruption of the M$_3$ before the P$_4$ in the mandible of *A. palliata* (lateral/buccal view). Note that the M$_3$ is fully erupted while the P$_4$ has not yet pushed the crown of dP$_4$ out of place, (c) Intraindividual variation in dental eruption sequence in *A. palliata* (palatal view). Note that the right P^4 is fully erupted while the left dP^4 has not yet been shed

Averages and ranges for each variable were collected from the published literature, with the exception of average maximum lifespans which were collected from AnAge, part of the Human Ageing Genomic Resources database (Tacutu et al., 2012), as well as from the Max Planck Institute of Demographic Research (Carey and Judge, 2000). All values, with the exception of litter size, were log-transformed for the analyses. The life history and body size traits included in this study are: maximum lifespan (years), average body mass of females (kilograms), average age at weaning (months), average litter size, average age at sexual maturity (females, years), average body length (centimeters), average age at eruption of mandibular M$_1$ (years), and average brain mass (grams).

We calculated phylogenetic independent contrasts across the phylogenetic tree using the *ape* package in R (Paradis, Claude, and Strimmer, 2004). This statistic allows for the comparison of means between traits while taking into account the phylogenetic relationships of 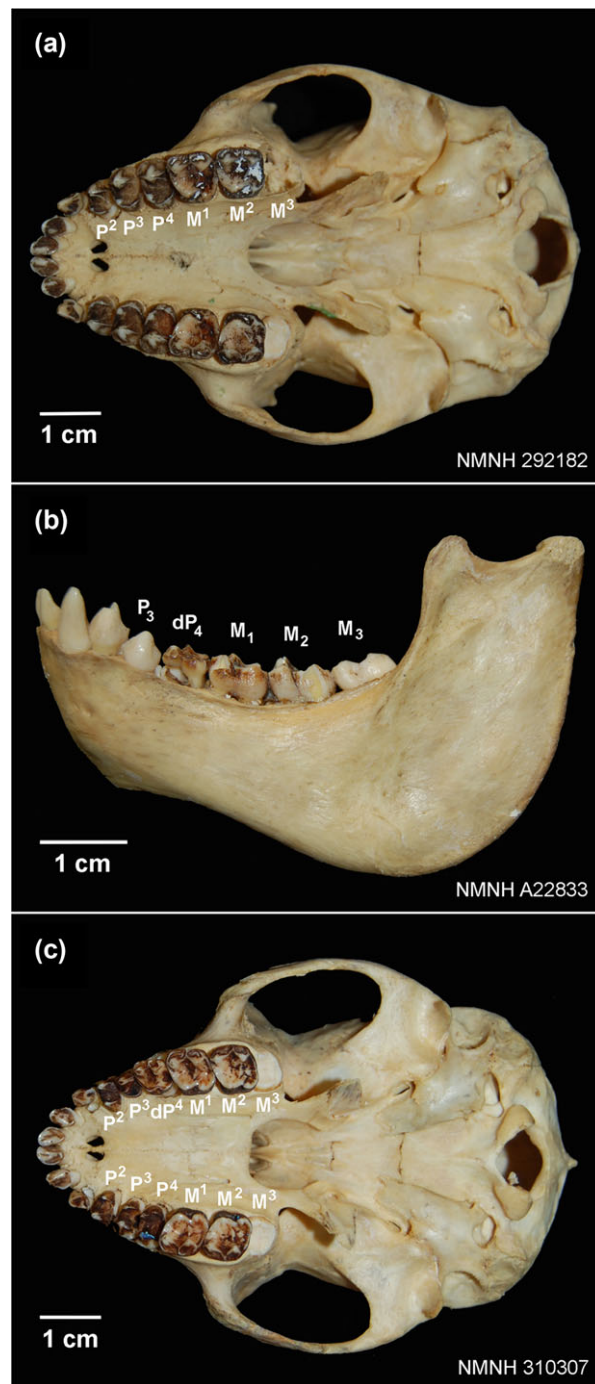the study taxa and the number of independent trait occurrences (Ricklefs and Starck, 1996). We ran the *D*-statistic in the R statistical program v3.1.2 (R Core Team, 2016) using *caper* (Orme et al., 2015) to test for phylogenetic signal in dental eruption

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TABLE 3 Primate and primate-outgroup dental eruption sequences

Clade	Family	Genus	Species	Sample size (n)	PM after M3[a]	M3 after PM	Variation
Catarrhini	Cercopithecidae	Allenopithecus	nigroviridis	1		X	
		Cercocebus	agilis	1		X	
			torquatus	11		X	
		Cercopithecus	aethiops	literature		X	
		Colobus	angolensis	1		X	
			guereza	4		X	
			polykomos	1		X	
			satanas	1		X	
			vellerosus	1		X	
		Erythrocebus	patas	3		X	
		Lophocebus	albigena	2		X	
		Macaca	mulatta	literature		X	
		Miopithecus	ogouensis	3		X	
		Nasalis	larvatus	literature		X	
		Papio	hamadryas	literature		X	
		Piliocolobus	badius	3		X	
		Presbytis	frontata	1		X	
			hosei	6	X		
			melalophos	3			X
			potenziani	2		X	
		Procolobus	verus	literature		X	
		Pygathrix	nemaeus	1		X	
		Semnopithecus	entellus	literature	X		
		Trachypithecus	cristatus	2		X	
			phayrei	1		X	
	Gorillidae	Gorilla	gorilla	literature		X	
	Hominidae	Homo	sapiens	literature		X	
	Hylobatidae	Hylobates	agilis	2		X	
			hoolock	1		X	
			klossii	2		X	
			lar	4		X	
			muelleri	4		X	
			pileatus	2		X	
			sp.	2		X	
		Symphalangus	syndactylus	2		X	
	Panidae	Pan	paniscus	literature		X	
	Pongidae	Pongo	pygmaeus	literature		X	
			Total	**67**	**2**	**34**	**1**
Platyrrhini	Aotidae	Aotus	trivirgatus	literature	X		
	Atelidae	Alouatta	palliata	14			X
			pigra	2		X	
			seniculus	12		X	
		Ateles	ater (sp.)	6		X	
			belzebuth	8		X	
			chamek	1		X	
			fusciceps	3		X	
			geoffroyi	10		X	
		Brachyteles	arachnoides	literature		X	
		Lagothrix	lagotricha	3		X	
	Callitrichidae	Callimico	goeldii	2			X

TABLE 3 (Continued)

Clade	Family	Genus	Species	Sample size (n)	PM after M3[a]	M3 after PM	Variation
	Cebidae	Cebus	albifrons	13		X	
			apella	19		X	
			capucinus	10		X	
			libidinosus[b]	6		X	
			olivaceus	6		X	
		Saimiri	sciureus	7			X
	Pitheciidae	Cacajao	calvus	literature		X	
		Callicebus	donacophilus	literature		X	
		Chiropotes	satanas	literature		X	
		Pithecia	monachus	1	X		
			Total	**123**	**2**	**17**	**3**
Strepsirrhini	Archaeolemuridae[c]	Archaeolemur[c]	sp. cf. edwardsi[c]	literature	X		
			majori[c]	literature	X		
		Hadropithecus[c]	stenognathus[c]	literature	X		
	Galagidae	Otolemur	crassicaudatus	literature	X		
	Indriidae	Avahi	sp.	literature		X	
		Propithecus	diadema (spp.)[d]	1		X	
	Lemuridae	Eulemur	fulvus	literature	X		
			mongoz[e]	literature	X		
		Lemur	catta	literature		X	
		Lepilemur	mustelinus (spp.)[f]	literature	X		
		Varecia	variegata	3	X		
	Lorisidae	Loris	tardigradus	literature	X		
		Nycticebus	bengalensis	literature	X		
		Perodicticus	potto	literature	X		
	Megaladapidae[c]	Megaladapis[c]	sp.	literature	X		
			Total	**4**	**12**	**3**	**0**
Tarsiiformes	Tarsiidae	Tarsius	bancanus	literature	X		
			spectrum	literature	X		
Adapiformes[c]	Adapidae[c]	Adapis[c]	parisiensis[c]	literature	X		
Plesiadapiformes[c]	Plesiadapidae[c]	Acidomomys[c]	hebeticus[c]	literature	X		
			Total	**NA**	**4**	**0**	**0**
Outgroup: Dermoptera	Cynocephalidae	Galeopterus	variegatus	8	X		
Outgroup: Scandentia	Ptilocercidae	Ptilocercus	lowii	literature	X		
	Tupaiidae	Tupaia	glis	literature	X		
			Total	**8**	**3**	**0**	**0**
GRAND TOTAL				**202**	**23**	**54**	**4**

[a] PM is premolars, M3 is third molar.
[b] NMNH catalogue lists this as hybrid species apella nigritus + libidinosus.
[c] Indicates an extinct taxon.
[d] Revised taxonomy has divided Propithecus diadema into multiple species (Groves and Helgen, 2007).
[e] Eulemur mongoz was previously published as Lemur mongoz (Schwartz, 1974; Tattersall and Schwartz, 1991).
[f] Revised taxonomy has divided Lepilemur mustelinus into multiple species (Rumpler and Albignac, 1978).

sequence. 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 < 1 indicates phylogenetic conservatism (Orme et al., 2015). As the D-statistic can only be applied to binary traits, and as the implications of variability in dental eruption sequence are still poorly understood, taxa with variable dental eruption sequence were

excluded from this phylogenetic analysis. The D-statistic relies on discrete classification and operates on binary traits, and a single discrete value representing dental eruption sequence was assigned to each species for this analysis. Larger sample sizes may further resolve intraspecific variation in dental eruption sequence and phylogenetic signal of this phenotype in primates.

We ran a Blomberg's K analysis using phylosignal in the picante package (Kembel et al., 2010) to test the phylogenetic signal of the

TABLE 4 Descriptive statistics for the primate life history and body size variables, by species

Life history/body size trait	PM erupt last				M3 erupts last			
	N=	Mean	Median	Range	N=	Mean	Median	Range
Average maximum lifespan (yr)	12	25.5	25.4	25.0	42	39.6	37.0	102.9
Average body mass (F, kg)	10	2.4	1.5	10.9	45	10.0	6.3	74.5
Average age at weaning (mos)	10	5.3	4.5	8.4	26	15.8	12.5	45.8
Average gestation time (days)	10	154.2	153.3	97.8	32	189.7	176.3	145.0
Average litter size	9	1.3	1.0	1.0	35	1.0	1.0	0.2
Average age at sexual maturity (F, yr)	8	2.0	1.9	2.7	23	6.8	4.7	28.8
Average body length (cm)	8	39.7	39.5	47.3	27	59.0	54.5	133.3
Average brain mass (F, g)	6	32.1	24.7	94.4	36	107.7	88.6	441.0
Average age at M_1 eruption (yr)	5	0.3	0.4	0.4	14	1.9	1.5	6.3

PM is premolars, M3 is third molar, N is species sample size, yr is years, F is female, kg is kilograms, mos is months, cm is centimeters, M_1 is mandibular first molar.

nonbinary life history and body size traits in this study. 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 1 generally indicates neutral evolution of the trait, while $K > 1$ generally suggests that the trait is highly conserved phylogenetically relative to Brownian motion. In contrast, $K < 1$ is generally interpreted as conserved phylogenetically, although less so than expected under a neutral conservation model, suggesting that selection pressures may be influencing the distribution of the trait. Alternatively, rapid divergence or heterogeneous rates of genetic drift can also result in a low K value (Blomberg, Garland, and Ives, 2003; Revell, Harmon, and Collar, 2008). Blomberg's K was used to test the phylogenetic signal of the continuous variables in this study, using mean values as reported in the literature and in online databases. As such, the method relies on the accuracy and precision of the reported values, and the use of larger sample sizes and a greater range of reported values may have some impact on the results of this analysis.

For these phylogenetic analyses, we trimmed the trees down to only those species for which dental eruption sequence was confidently assessed and invariable, and for which molecular data were available. We ran both the D-statistic and Blomberg's K through 25 iterations, using 25 of the likely phylogenies generated by the 10kTrees analyses to account for phylogenetic uncertainty. The average of the 25 iterations was taken as the value of D and K for analysis of phylogenetic signal.

We ran an ancestral state reconstruction using the distribution of extant dental eruption sequences across the primate phylogeny to quantify the evolutionary context of dental eruption sequence. Also known as character mapping, ancestral state reconstruction statistically predicts the state of each node in the phylogeny based on the distribution of a character across the tips (Coddington, 1988; Donoghue, 1989; Felsenstein, 1985). For this reconstruction, we mapped dental eruption sequence onto the primate phylogeny by creating a character state matrix. We ran the ancestral state reconstruction in Mesquite with Mk1 likelihood (Maddison and Maddison, 2016). 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, 2016). In cases where we have phenotypic data for a species, but molecular data are not available, we used congeners in the phylogeny (marked by an asterisk), or manually added the species into the phylogeny.

It is important to note that debate continues about phylogenetic relationships among crown primates. In particular, the relationship of tarsiers relative to anthropoids and strepsirrhines has been a source of controversy (Gingerich, 1981; Kay and Ungar, 1997; Simons and Rasmussen, 1989; Szalay and Delson, 1979). Most recently, molecular data have been used to place tarsiers and anthropoids into a single clade, the haplorhines (Jameson et al., 2011; Schmitz, Ohme, and Zischler, 2001). Following the molecular data, the divergence of strepsirrhines is placed basal to tarsiers and anthropoids 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 ~42–50 MA, and the divergence of apes and Old World monkeys is estimated at approximately 30 MA (Steiper and Young, 2006).

TABLE 5 Phylogenetic independent contrasts between dental eruption sequence and life history/body size traits in primates[a]

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 brain mass (F, g)	**0.044**
Average age at M_1 eruption (yr)	0.259

[a] Yr is years, F is female, kg is kilograms, mos is months, cm is centimeters, g is grams, M_1 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 Starck, 1996). PICs in bold are significant.

TABLE 6 Tests of phylogenetic signal in primates[a]

Life history/body size trait	Blomberg's K	K p-value	D statistic	D p-value
PM erupt after M3	–	–	−0.123	0.379
Average brain mass (F, g)	2.515	**0.001**		
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	–	–

[a] All bolded p-values are significant. PM is premolars, M3 is third molar, M_1 is mandibular first molar, yr is years, F is female, kg is kilograms, cm is centimeters, mos is months. Raw data for life history and body size traits are available in Supporting Information Appendix G.

3 | RESULTS

We definitively assessed dental eruption sequence in 21 genera and 46 species. We also culled dental eruption sequence data from the literature for an additional 29 genera and 32 species to bring the total number of primate genera and primate species sampled to n = 50 and n = 78, respectively (Table 3). This sample encompasses all major primate clades. We also compiled data on three outgroup species to primates, through investigation at the NMNH (Dermoptera: *Galeopterus variegatus*, n = 8), and from the literature (Scandentia: *Ptilocercus lowii*, *Tupaia glis*).

3.1 | Intraspecific variation

Of the n = 849 *Cebus* specimens, n = 62 were in the process of erupting one or more of the postcanine teeth at the time of death. These 62 specimens span seven species of *Cebus*, as well as one hybrid species listed as *Cebus apella* + *libidinosus*, and have erupted both the first or second molars, but the premolars and/or third molar are still unerupted. None of these specimens were found to have erupted the third molar prior to the premolars (Supporting Information Appendix C). The average scores for the entire sample support a dental eruption sequence of M_1, M_2, $[P_4, P_3, P_2]$, M_3. The premolars are listed in brackets due to observed variation between species (e.g., female *Cebus capucinus* specimens NMNH 306828 and NMNH 291230). Both the average and median of the sample support that the third molar erupts last in all species of *Cebus*.

3.2 | Interspecific variation

Primate specimens sampled here fall into 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. Of this large sample of primates, n = 54 species erupt the third molar after the premolars, n = 20 erupt one of the premolars after the third molar, and n = 4 species show variation in dental eruption sequence.

We sampled 59 extant anthropoid (catarrhine + platyrrhine) species, and 51 of these species erupt the third molar after the premolars.[1] In contrast, eight of the 11 extant strepsirrhine species sampled erupt one of the premolars after the third molar. The exceptional anthropoid taxa that erupt one or more of the premolars after the third molar are *Aotus trivirgatus*, *Pithecia monachus*, *Presbytis hosei*, and *Semnopithecus entellus*, while four anthropoid taxa exhibit intraspecific variation in dental eruption sequence: *Alouatta palliata*, *Callimico goeldi*, *Presbytis melalophos*, and *Saimiri sciureus* (Supporting Information Appendices D–F). 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, *Avahi* sp., *Lemur catta*, and *Propithecus diadema* (spp.) are unique in erupting the third molar after the premolars. Studies of fossil indriids and palaeopropithecids suggest that these taxa have a dental eruption sequence similar to living Indriidae (*Avahi* and *Propithecus*), where the third molar erupts after the premolars (e.g., Godfrey, Petto, and Sutherland, 2002). However, different eruption sequences have been published for *Lemur catta*, with Schwartz (1974) reporting the third molar erupting after the last premolar, and with King, Godfrey, and Simons (2001) reporting at least one premolar erupting after the third molar, as in other lemurids, and indeed most lemurs. Dental eruption sequences for *Avahi* sp. and *Lemur catta* were taken from the literature (Table 3), but the eruption sequence for *P. diadema* (spp.) was collected by TM during this study.

3.3 | Phylogenetic analyses

We were able to collect life history and body size data for between five and 12 species, depending on the variable, of the 20 primate species that erupt one of the premolars after the third molar in this study. We also collected data for a minimum of 14 and maximum of 48 primate species that erupt the third molar after the premolars, again depending on the life history or body size variable (Table 4, Supporting Information Appendix G). Data on average age at M_1 eruption were available for the fewest primate species relative to the other life history and body size variables sampled here. In contrast, average maximum lifespan, body mass, age at weaning, and litter size are the variables with the best coverage across the phylogeny.

The only life history or body size variables found to be significantly correlated with dental eruption sequence in primates are average body mass and brain mass (Table 5). The phylogenetic independent contrast for average age at sexual maturity approaches statistical significance (p = 0.08), but all of the other traits, including the life history variables, are far from significant. These data indicate

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[1]There were some primate genera for which only one specimen was available at the correct ontogenetic stage to evaluate dental eruption sequence: *Allenopithecus*, *Pithecia*, and *Pygathrix* (Table 3).
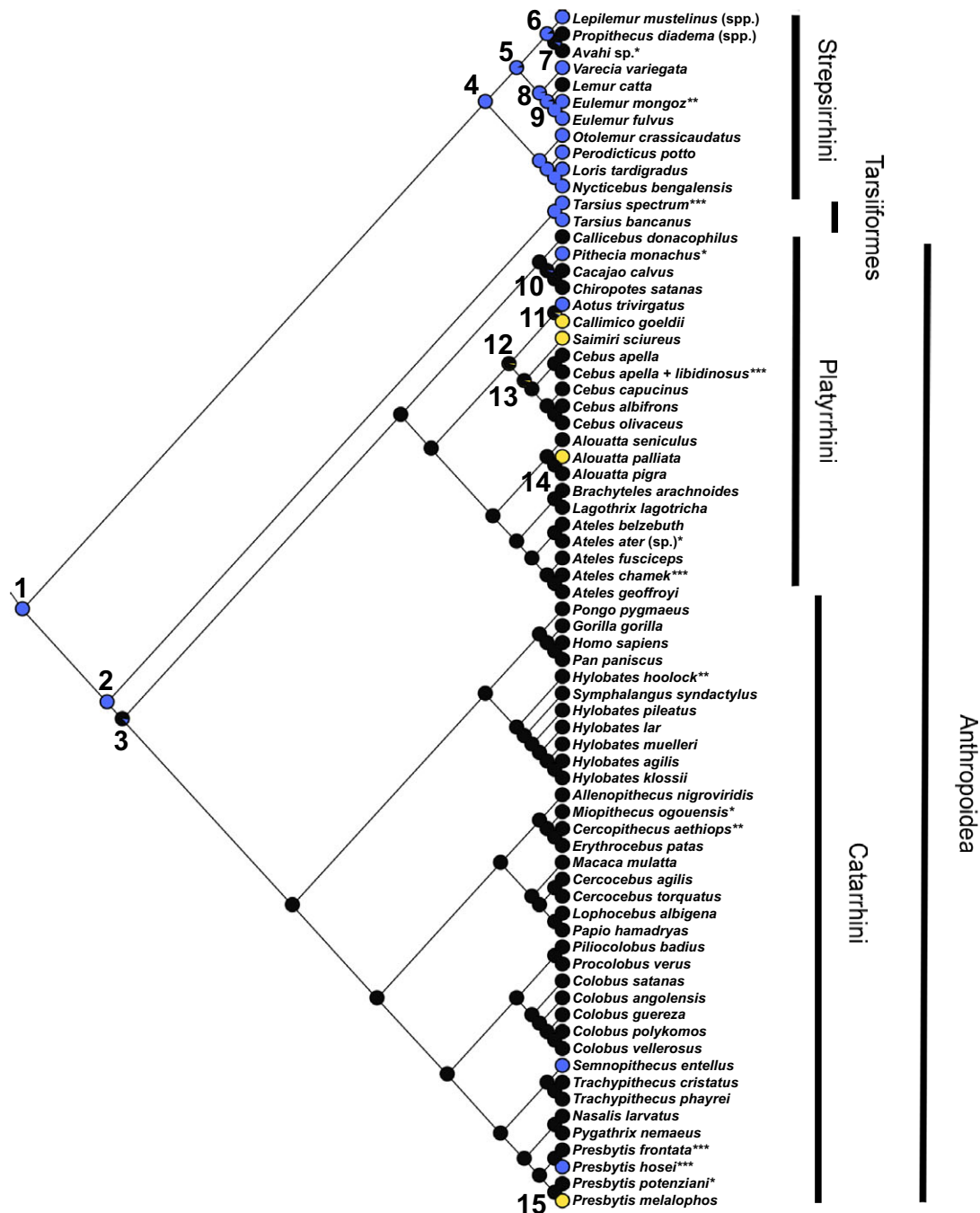
FIGURE 3 Results of the maximum likelihood ancestral state reconstruction in primates. Black indicates that the third molar erupts after the premolars. Blue indicates that the third molar erupts before one or more of the premolars. Yellow indicates that there is intraspecific variation in the sequence 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 or updated genus-level classification. A triple asterisk denotes taxa that were manually added into the phylogeny. See Table 7 for dates at numbered nodes

that, independent of phylogeny, body mass and brain mass are correlated with dental eruption sequence.

Our results also show that dental eruption sequence is conserved phylogenetically and has phylogenetic signal in primates ($D = -0.123$, Table 6). This signal is not significantly different than what is expected under a neutral model of conservation ($p = 0.379$), a result that is likely driven by the species that deviate from the

dominant pattern in their clade (e.g., *Propithecus diadema* (spp.), *Semnopithecus entellus*). The majority of primate life history and body size variables analyzed here also have significant phylogenetic signal ($p < 0.05$), meaning that the distribution of each trait across the phylogeny is more conserved (i.e., variation matches changes in the phylogeny) than expected under a neutral model of Brownian motion (Table 6). The variables that do not exhibit significant phylogenetic

TABLE 7 Likelihood (%) of each dental eruption sequence at each ancestral state node on the primate phylogeny[a]

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	~30 MA	Kistler et al. 2015
6	10.92%	88.18%	0.90%	Indriidae	~20 MA	Kistler et al. 2015
7	90.13%	8.84%	1.03%	*Propithecus*	~15 MA	Kistler et al. 2015
8	5.26%	94.41%	0.33%	*Varecia*	~20 MA	Kistler et al. 2015
9	7.20%	92.35%	0.45%	*Lemur catta*	~15 MA	Kistler et al. 2015
10	94.58%	5.08%	0.34%	*Pithecia*	~13 MA	Opazo et al. 2006
11	91.30%	3.37%	5.34%	*Aotus*	~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%	*Saimiri*	~17 MA	Opazo et al. 2006
14	98.74%	0.02%	1.24%	*Allouata palliata*	~6 MA	Perelman et al. 2011
15	97.48%	0.18%	2.34%	*Presbytis melalophos*	~6.5–8 MA	Sterner et al. 2006

[a] ASR Node refers to Figure 3. ASR is ancestral state reconstruction, M3 is third molar, PM is premolars. There are some disagreements about the exact branching order of the phylogeny.

signal are average body length and average age at weaning. Of the life history and body size variables, average brain mass has the most conserved phylogenetic signal (K = 2.52), followed by average age at M_1 eruption (K = 2.29).

Average body mass also has a high K value, indicating highly conserved phylogenetic signal for this variable.

3.4 | Ancestral state reconstruction

Ancestral state reconstruction suggests that one of the premolars, rather than the third molar, erupted last in the ancestor of Primates with 97.8% likelihood (Figure 3). 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 tarsiiformes, the ancestral state reconstruction supports the hypothesis that the ancestor of anthropoids 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 7.

4 | DISCUSSION

The data presented in this study make some clear statements about dental eruption sequence in primates, and likely other mammals. Dental eruption sequence in primates is conserved phylogenetically as attested by both the distribution of sequences across the phylogeny of extant taxa, as well as through the statistical testing of phylogenetic signal using the *D*-statistic. This conserved phylogenetic signal is consistent with many studies on dental eruption sequence in primates (e.g., Byrd, 1981; Godfrey, Samonds, Wright, and King, 2005; Schwartz, 1974; Tattersall and Schwartz, 1974), and, more recently, in

artiodactyls (Monson and Hlusko, 2016; Veitschegger and Sánchez-Villagra, 2016). Based on our ancestral state reconstruction, the two major primate clades (Strepsirrhini and Anthropoidea) have different ancestral dental eruption sequences. Ancestral state reconstruction suggests that the premolars erupted after the third molar in the ancestor of primates, and that dental eruption sequence changed from one where the third molar erupted before the premolars, to one where the third molar erupted after the premolars in the ancestor of anthropoids, sometime after the divergence of the tarsiers in the Eocene (Beard, 2002). Within anthropoids, there are several taxa that are exceptional in having a dental eruption sequence that is consistent with the ancestral condition. These likely represent secondarily derived sequences. The incorporation of additional fossil evidence will likely further refine estimates of the timing of the evolution of dental eruption sequences. Based on craniodental morphology, and the results of the phylogenetic independent contrasts tested in this study, we have several possible hypotheses about the drivers of dental eruption sequence in primates.

4.1 | Body size and brain mass

Body size and brain mass are not life history traits per se, as they represent adult phenotypes. However, we included them in our analyses because they are key traits in primate evolution and represent the ultimate outcomes of ontogeny. We find that the relationship between adult body size and dental eruption sequence in primates is significant, and it is most visible 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.

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, Supporting Information Appendix G). 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., Grieco, Rizk, and Hlusko, 2013; Willis and Swindler, 2004). 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.

Brain mass is also significantly correlated with dental eruption sequence in this study, supporting a relationship between body size and brain mass in primates more generally (e.g., Gould, 1975). Our data demonstrate that both body size and brain mass are conserved phylogenetically, and both traits are significantly correlated with dental eruption sequence in primates. Body size and brain mass are both extremely important phenotypes in primate evolution and ecology, and while correlations between these phenotypes and dental eruption sequence are only beginning to be recognized, future research on associations between these variables will further illuminate the nature of their genotypic and phenotypic relationships.

4.2 | Fusion of the mandibular symphysis

We also see in our results a general correlation between fusion of the mandibular symphysis and dental eruption sequence. This relationship has also been noted in artiodactyls (Monson and Hlusko, 2016). Symphyseal fusion is thought to have evolved convergently multiple times in primates as an adaptation to increasing jaw muscle force and control (e.g., Hylander, Ravosa, Ross, and Johnson, 1998; Lieberman and Crompton, 2000; Ravosa, 1999; Tattersall 1973, 1974). 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, Tong, Dawson, Wang, and Huang, 1996). This state is shared with many omomyids and adapiformes, although, some adapiformes, such as *Silvaladapis*, 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 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). As such, the fossil record suggests that symphyseal fusion evolved early in the anthropoid lineage (Rasmussen and Simons, 1992; Ravosa, 1999; Simons 1989).

Extant strepsirrhines have unfused mandibles, while extant anthropoids have fused mandibles (Hylander, Ravosa, Ross, Wall, and Johnson, 2000; Hylander et al., 1998, 2004; Lieberman and Crompton, 2000; Williams, Kay, and Kirk, 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 molar after the premolars, while taxa with unfused symphyses erupt the third molar before one or more of the premolars. This same pattern is seen in artiodactyls (Monson and Hlusko, 2016). Deviations from this correlation may be representative of strong evolutionary and ecological pressures resulting from changes in diet and/or body size.

When examining 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) notes that the evolution of a fused mandibular symphysis in the Eocene fossil primate *Notharctus* seems to occur in step with increasing body size, while *Smilodectes* maintains small body size and an unfused mandibular symphysis. Likewise, studies of extinct lemuriformes show that the mandible fused in the largest extinct species and remained unfused in the smaller-bodied, extinct lemurs (Ravosa 1991, Ravosa, Stock, Simons, & Kunwar, 2007, Ravosa and Simons, 1994, King et al., 2001).

Based on the results of our study, there appears to be some relationship between body size, mandibular fusion, and dental eruption sequence in primates. While speculation on the evolutionary or mechanical pressures symphyseal fusion may have on dental eruption sequence, if any, is beyond the scope of this study, we note here the superficial correlation between these phenotypes. While there are some incidences of reversal, or secondary derivation, of dental eruption sequence in extant primates, there are no known cases of reversal from a fused mandible to an unfused mandible in these primate taxa. Future studies that further incorporate fossil primates will likely contribute to a better understanding of the relationship between body size, mandibular symphyseal fusion, and the evolution of dental eruption sequence.

5 | CONCLUSION

This study is the most comprehensive collection of dental eruption sequences in primates to date, and the evidence strongly supports that eruption sequence is phylogenetically conserved in primates and is not correlated with life history, contrary to the hypothesis postulated by Schultz's rule. Dental eruption sequence is, however, significantly correlated with average adult body size and brain mass in primates. This correlation is driven by the strepsirrhines and tarsiiformes, as well as several platyrrhine taxa.

This study 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., Asher and Olbricht, 2009; Billet and Martin, 2011; Dirks et al., 2009, Franzen et al., 2009; Loe et al., 2004; Macho and Williamson, 2002; Robson and Wood, 2008; Townsend and Croft, 2010; Yamanaka et al., 2010). However, more intensive testing of Schultz's rule, with a larger sample of more phylogenetically diverse primates, shows that correlations between dental eruption sequence and life history dissipate. Dental eruption sequence, life history traits, and brain and body size all carry conserved phylogenetic signal. Only

brain and body size are correlated with dental eruption sequence when phylogeny is taken into account, and these are likely serving as proxies for as-yet unidentified ontogenetic processes. However, dental eruption sequence is conserved phylogenetically and is therefore informative in yielding insight into taxonomic debates. Overall, our results suggest that body size and mandibular symphyseal fusion may have intertwined influences on the evolution of dental eruption sequence in primates.

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