

Dental Eruption and Growth in Hyracoidea (Mammalia, Afrotheria)

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ABSTRACT---We investigated dental homologies, development, and growth in living and fossil hyracoids, and tested if hyracoids and other mammals show correlations between eruption patterns, gestation time, and age at maturity. Unlike living species, fossil hyracoids simultaneously possess replaced P1 and canine teeth. Fossil species also have shorter crowns, an upper and lower I3 locus, an upper I2, and a hypoconulid on m3. Prenatal specimens of the living *Procavia capensis* and *Heterohyrax brucei* show up to three tooth buds posterior to upper d11 and anterior to the seven upper cheek teeth that consistently erupt; these include an anterior premolar but not a canine. Most lower cheek teeth finish eruption during growth in hyracoids, not after growth as in most other afrotherians. All hyracoids show the m1 at (lower) or near (upper) the beginning of eruption of permanent teeth; M3/m3 is the last permanent tooth to erupt. The living *P. capensis* erupts most lower antemolar loci before m2. In contrast, fossil hyraxes erupt lower antemolars after m2. While the early eruption of antemolars correlates with increased gestation time and age at maturity in primates and *Tupaia* (i.e., "Schultz's Rule"), and while modern hyraxes resemble some anthropoid primates in exhibiting long gestation and eruption of antemolars at or before molars, eruption patterns do not significantly co-vary with either life history parameter among afrotherians sampled so far. However, we do observe a shift in eruption timing and crown height in *Procavia* relative to fossil hyracoids, mirroring observations recently made for other ungulate-grade mammals.

PLAIN LANGUAGE SUMMARY---Our work examines how teeth erupt in living and fossil hyraxes (also known as dassies) and how they differ from their extinct relatives and other mammals. Fossil hyraxes differ from living ones in showing baby teeth for the first premolar and canine, and in having shorter tooth crowns. Hyrax fetuses help us to identify the first molar-like tooth that consistently erupts as a premolar, not a canine. Most of the permanent teeth erupt and are in use while hyraxes are growing, not after they reach adult size as in hyrax relatives like many tenrecs, golden moles, sengis, and manatees. In hyraxes the first molar is generally the first permanent tooth to erupt, and the last molar erupts after all of the others. Living hyraxes have fewer teeth in the front of the jaws and show eruption of several other permanent teeth prior to the second molar. In contrast, fossil hyraxes erupt most of their permanent teeth after their second molar. The eruption of some teeth with or before the molars correlates with a longer pregnancy time and age at maturity in primates, and living hyraxes resemble the eruption patterns and long pregnancies seen in some monkeys and humans. Mammals more closely related to hyraxes do not show such correlations, but eruption timing does correlate with increased crown height in living hyraxes, an association recently made by other investigators for certain fossil rhinoceroes and extinct mammals native to South America.

INTRODUCTION

Living hyraxes, or dassies (Procaviidae, Hyracoidea, Afrotheria), consist of three genera and four species: *Procavia capensis*, *Heterohyrax brucei*, *Dendrohyrax arboreus*, and *Dendrohyrax dorsalis* (Shoshani 2005). Adults average between 2-4kg; males of *P. capensis* can approach 5kg in body mass. All are semi- to very gregarious herbivores found in arid and forested habitats. They are almost entirely African in their extant distribution. *P. capensis* is the most widespread, from South Africa into the Arabian peninsula and Levant (Fischer 1992; Nowak 1999). Hyracoids were much more diverse in the geological past, including forms convergent upon antelopes (*Antilohyrax*), rhinos (*Titanohyrax*), suids (*Geniohyus*), and a late Eocene/early Oligocene genus with a pneumatized, sexually dimorphic mandibular resonating chamber (*Thyrohyrax*; see Schwartz et al. 1995; Rasmussen & Simons 2000; DeBlieux et al. 2006). Some aspects of their anatomy are similar to perissodactyls (Fischer 1992), but they are not closely related to them, beyond their status as placental mammals. Hyracoids belong in Afrotheria along with proboscideans, sirenians, *Orycteropus*, macroscelidids, tenrecids, and chrysochlorids (Murphy et al. 2001; Asher & Seiffert 2010; Tarver et al. 2016).

Hyracoids have a good fossil record, including postnatal growth series of two genera known from near the Eocene-Oligocene boundary in Egypt: *Thyrohyrax* and *Saghatherium*. Ongoing paleontological work over several decades (Bown et al. 1982, 1988; Rasmussen & Simons 1988; Gheerbrant et al. 2007; Tabuce et al. 2007; Seiffert 2006, 2007; Rasmussen & Gutierrez 2010; Barrow et al. 2010, 2012; Tabuce 2016) has uncovered thousands of individual hyracoid fossils, and these two taxa are among the most common fossils recovered at Paleogene sites in northern Africa. While the vast majority are fragmentary, several are more complete and represent a

number of distinct ontogenetic stages. Here, we take advantage of this collection in order to investigate their growth and dental homologies. We combine our observations on these fossils with data on growth and dental eruption among living hyraxes and other taxa in order to investigate the pattern and process of dental eruption in mammals.

Dental ontogeny in *Procavia capensis*

Studies of dental eruption in the extant rock hyrax (*Procavia capensis*) are based on populations from the Levant (Roche 1978) and South Africa (Fairall 1980; Fourie 1983; Steyn & Hanks 1983; Fisher & Parkington 2014), as summarized in Table 1. These authors assumed a full dental formula of 1.0.4.3/2.0.4.3 (incisors.canines.premolars.molars; see below and Fig. 1). According to Fourie (1983; see also Fischer 1992: table 62), the earliest, approximate chronological age of hyraxes when the lower dp4, m1, m2, and m3 finish erupting is (respectively) 5, 13, 21, and 49 months post-birth. Upper teeth tend to erupt after their lower counterparts, and the upper M3 finishes erupting around 60 months post-birth, notably comprising about half of this animal's typical 10-12 year lifespan. Roche's (1978) eruption data from the upper toothrow are mostly consistent with Fourie (1983), with the exception of the upper premolars. According to Roche (1978), upper premolars erupt after M1 but before M2, whereas Fourie (1983: table 17) implies that they erupt prior to M1. Fairall (1980: table 4) gave eruption data for a captive South African population of *P. capensis*, fed a mixture of alfalfa and commercial rabbit feed. He reported the lower m1 as the first to erupt, followed by i1-2, p1-2, m2, then p3, then m3 in the dentary. Strangely, he depicted the lower p4 locus as absent ("no tooth" in his table 4) throughout growth; to our knowledge no other author has ever

claimed that *P. capensis* lacks a lower p4, nor have we seen any specimen that lacks one. In the upper dentition, he reported M1 as the first to erupt, followed by I1 and P1-2, then P3-4, then M2, then M3.

This eruption sequence is generally consistent with that of Fourie (1983), except that in the lower dentition p3 and m2 are switched, and that Fairall (1980) neglects the p4 locus. Fairall's (1980) sequence for the upper dentition shows an earlier eruption for M1 (ahead of I1 and the premolars) compared to Fourie (1983). Even more discrepant are Fairall's (1980) much earlier timings for eruption at the m1 and m3 loci, which he claimed to have observed in the lower dentition at (respectively) two and 24 months. However, Fairall (1980:21) noted that "criteria for a fully erupted tooth were different" and that "it is possible that M³ was not fully erupted at 36 months" (compared to over 60 months reported by Roche, 1978), without further elaboration. Despite these discrepancies, and for wild populations, Fourie (1983: 97) wrote that "provided the date of collection within the study area is known, hyrax skulls up to the age of 36 months can be aged with a high degree of accuracy (to within ± 1 month) using eruption and replacement criteria."

Although Fairall (1980) and Fourie (1983) did not report identical values for ages at molar eruption, they did report mutually consistent patterns of skull growth. Fairall (1980: table 2) reports cranial metrics for hyraxes of known ages between 1 day and 36 months; Fourie (1983: table 22) provided similar data for hyraxes between 12 and 108 months, as depicted in supplementary Fig. S1. Where the ages overlap in the two studies (one to three years), reported jaw lengths also overlap, growing from ca. 60mm at year one to just over 70mm at year three, when both male and female hyraxes greatly slow their rates of growth (Fig. S1). Moreover, the skull metric-age regression equations given by Fourie (1983: table 23) provide estimates

of age derived from jaw lengths that (as expected) fit reasonably on the curve that represents actual ages.

Hyracoid dental homologies

The authors above treated the anterior-most permanent tooth typically found in the maxilla of fully grown *Procavia* as the P1, not canine. The character matrix of Seiffert (2007) treated the *Procavia* lower p1 as polymorphic, the upper P1 as present, and the lower and upper canines as absent (his characters 18, 102, 14, and 97, respectively). Therefore, these authors either stated or implied the dental formula of *Procavia* to be 1.0.4.3/2.0.4.3 (Fig. 1).

In contrast, based primarily on data from five histologically sectioned embryos ranging in size from 19.5 to 60mm CRL (crown rump length), Lockett (1990, 1993) argued for the homology of the anterior-most, upper cheek tooth of *Procavia* as the canine, not P1, and his proposal has been followed by some subsequent authors (e.g., Fischer 1992; Asher & Lehmann 2008). According to Lockett (1993: 279-280), "ontogenetic analysis of *Procavia* fetuses reveals that only three maxillary teeth develop anterior to dP4. The homology of the anteriormost of these as dC is corroborated by its initiation at the rostral extent of the maxilla" (pp. 279-280). Fischer (1992 erratum), following Lockett (1990, 1993), also identified the four lower premolariforms in *P. capensis* as a canine followed by p2-4, therefore giving a dental formula of 1.1.3.3/2.1.3.3.

This interpretation contrasts with Roche (1978), Fourie (1983), and Seiffert (2007) who identified the four loci between i2 and m1 in the dentary of postnatal specimens as premolars, although Roche (1978) noted that the anterior-most of these is frequently missing in the lower dentition: "Only rock hyraxes of southern

Africa (*P. capensis*), with a few rare exceptions, possess no more than three premolars in each lower half-jaw, through the non-replacement of the first deciduous premolar. Similarly, among many *Procavia*, particularly in northeast Africa, there is a very significant propensity for atrophy via the loss of the first lower premolar, and in some cases its superior counterpart. Finally, the upper canine may still persist in the teeth of some adult hyraxes"¹ (Roche 1978:98).

Unlike extant *Procavia*, the dental formula for both *Saghatherium* and *Thyrohyrax* is relatively straightforward because these taxa possess a full dentition for a placental mammal. That is, there are five replaced, non-incisiform teeth anterior to the three molars in both upper and lower dentitions, consisting of a canine followed by four premolars. These are posterior to three upper and three lower incisors (Gheerbrant et al. 2007; Seiffert 2007). Hence, the dental formula for both genera is 3.1.4.3/3.1.4.3. Moreover, Gheerbrant et al. (2007: fig. 9) provide good evidence for replacement of upper and lower P1 and canine loci in *Saghatherium antiquum*, making this taxon among the very few with demonstrable replacement at the first premolar locus (Uhen 2000; van Nievelt & Smith 2005). Barrow et al. (2010) also identified isolated teeth as dP1 and P1 in the earliest late Eocene hyracoid *Dimaitherium*.

Dental ontogeny and life history

"Schultz's Rule" (Schultz 1956, 1960; Smith 2000; Schwartz 2012) is the proposition that species with relatively slow development, i.e., those that are slow to mature and have a long gestation period, erupt more antemolars before molars

¹ "Seuls les damans de rochers du sud de l'Afrique (*P. capensis*), à quelques rares exceptions près, ne possèdent plus que trois prémolaires par demi-mâchoire inférieure, par suite du non-replacement de la première prémolaire lactéale. De même, chez nombre de *Procavia*, en particulier du nord-est de l'Afrique, il y a une très nette propension à l'atrophie, puis à la perte de la première prémolaire inférieure, voire dans certains cas de son homologue supérieur. Enfin, la canine supérieure peut encore persister dans la denture définitive de certains damans."

compared to their common ancestors with faster development. Schultz inferred that the primate common ancestor exhibited a scandentian (*Tupaia*)-like ontogeny and life history, with rapid growth following a brief gestation period. *Tupaia* also exhibits eruption of all three molars prior to incisors and premolars. In lemurid primates, at least the toothcomb (consisting generally of i1-2 and the canines) and in some cases also one or more premolars erupt prior to m2; among some platyrrhine primates (e.g., *Cebus*) incisors erupt prior to m2; in humans incisors erupt simultaneously with or even prior to m1, and the remaining antemolars erupt prior to m2 and m3. Schultz argued that these groups exhibited a corresponding change of life history, towards later age at sexual maturity, longer gestation times, and a longer lifespan. He reasoned that in order to extend the utility of an effective, functional dentition over a long lifespan, there would have been selective pressure to delay eruption of posterior teeth so that the antemolars appear to erupt earlier. Stated differently, the later M2 and M3 erupt, the more useful they will be as the animal ages during an extended lifespan, and the higher the probability that antemolars will erupt before them.

A number of authors have examined patterns of dental eruption in mammals (e.g., Ziegler 1972; Asher & Lehmann 2008; Böhmer et al. 2016) and some have tested the applicability of Schultz's Rule (Smith BH 2000; Godfrey et al. 2005; Guthrie & Frost 2011; Jordana et al. 2013; Geiger et al. 2016; Monson & Hlusko 2016; Smith TD et al. 2015; Veitschegger et al. 2016). In brief, there is some evidence for a correlation between at least some life-history variables and dental eruption in primates (Smith BH 2000) and some caprine artiodactyls (Jordana et al. 2013), although the "rule" does not appear to apply generally among artiodactyls (Monson & Hlusko 2016; Veitschegger et al. 2016) or canid carnivorans (Geiger et al. 2016). Among primates, a number of exceptions exist (Godfrey et al. 2005;

Guthrie & Frost 2011). Nonetheless, given the potential to infer paleontologically elusive aspects of growth and development in fossil hyracoids, it is worth investigating the extent to which dental development correlates with life history parameters such as gestation time and age at maturity among afrotherians.

MATERIALS AND METHODS

Here, we seek to document the pattern of replacement in ontogenetic series of fossil hyracoids, to use their dental morphology and ontogeny to clarify the ambiguities surrounding dental homologies in extant hyracoids, and to test potential correlations between life history and eruption pattern in afrotherians and other mammals. We therefore assembled a dataset of dental metrics and growth, consisting of microCT scans (Table S1) of living hyraxes and fossil hyracoids known primarily from Quarry L-41 (Jebel Qatrani Formation, latest Eocene, ~34 Ma; Seiffert 2006) in the Fayum Depression, Egypt. These consisted of the genera *Sagatherium* and *Thyrohyrax*, best known for the species *S. boweni* and *T. meyeri*. In addition, we examined CT scans of a *Microhyrax* jaw from the late Early or early Middle Eocene of Gour Lazib (Algeria), three *T. litholagus* jaws from Quarry L-41, two of *S. antiquum* from the early Oligocene of quarries F and B-2, one of *T. domorictus* from the early Oligocene of Quarry L-46, and observations on numerous other living and fossil hyracoids. We have made our tomographic scans of *Procavia* and Fayum hyracoids housed at the University Museum of Zoology Cambridge (UMZC) and Duke Primate Center (DPC) accessible at morphosource.org (see Table S1 for DOI numbers). Species definitions and distributions of fossil hyracoids followed Rasmussen and Gutierrez (2010). Museum collections identified in Table 2 and the literature (Smith 2000; Godfrey et al. 2005; Asher & Lehmann 2008; Asher &

Olbricht 2009; Guthrie & Frost 2011) enabled us to quantify dental eruption patterns in afrotherians, primates and *Tupaia*.

Where possible, measurements were taken to the nearest 0.1mm using 3D reconstructions of CT scans using the "path" command on Drishti 2.6.2 (Limaye 2012), with camera type set to orthographic. CT-derived metrics were supplemented by measurements taken with hand-calipers. Some metrics (e.g., symphysis-condyle length) exhibited 0-1% differences in CT vs. hand-caliper derived measurements. Other metrics (e.g., M1 width) occasionally reached up to 12% difference in some cases (Supplementary Datafile 1A). Therefore, where possible we avoided combining the two measurement techniques to quantify any single variable. Due to the lack of CT scans for specimens of *T. meyeri* with a fully erupted m3, we used calipers to measure median posterior symphysis-anterior coronoid length in such *T. meyeri* specimens, and used this to standardize posterior symphysis-anterior coronoid lengths for *T. meyeri* specimens showing incompletely erupted m3 loci measured from CT scans. We also used caliper measurements to quantify m1 area in living and fossil hyracoids, the differences between which are relatively the same regardless of measurement technique. Figure 1 shows the dimensions used to define our measurements; supplementary datafile 1A-G provides our raw data.

Following Asher & Lehmann (2008), eruption status taken from direct observations on museum specimens were binary: a given permanent tooth locus was either fully erupted (1) or not (0). For specimens sampled using CT, we identified six categories of dental eruption: 1) at least partly mineralized deciduous tooth largely or entirely in crypt, 2) partly erupted deciduous tooth, 3) erupted deciduous tooth with the enamel-dentine junction (EDJ) at the alveolar plane, 4) at least partly mineralized permanent tooth in crypt present simultaneously with erupted deciduous

tooth, 5) partly erupted permanent tooth adjacent to the deciduous precursor, and 6) fully erupted permanent tooth with the EDJ at the alveolar plane. We further qualified categories 4 and 5 with "a" when a tooth was missing but its presence could still be inferred based on the alveolus, or "m" in the case of molars (which lack deciduous precursors). We placed every available locus of the specimens listed in Supplementary Datafile 1B into one of these six categories, along with two indices of overall size: posterior condyle to anterior symphysis length (where possible) and anterior coronoid to posterior symphysis length (Fig. 1). We used the latter measurement to quantify growth, as it does not depend on the rare preservation of an intact mandibular condyle and anterior symphysis and is more frequently available in fossil specimens.

We then quantified the proportion of erupted teeth in each specimen by summing the values described above (1-6) for each of N available tooth loci, and dividing this sum by the maximum possible for a fully grown individual with N loci (i.e., $6N$). This yields a range of 0-1 for any given specimen where 0 represents no erupted teeth and 1 represents all erupted, permanent teeth. For example, DPC 11919 (*S. boweni*) has fully erupted dp1-4 (with no signs of mineralized p1-4 in their crypts), fully erupted m1, and m2 within its crypt. This is represented as 3-3-3-3-6-4 and sums to 22; out of a possible 36 (for six loci) this specimen has an eruption ratio of 22/36 or 0.61. Another specimen of *S. boweni* (DPC 20173) consists of dp2-4 and a partly erupted m1, represented by 3-3-3-5, yielding 14/24 or 0.58, a lower value that reflects the more dentally immature status of DPC 20173 compared to DPC 11919. This metric has the disadvantage of being sensitive to number of known tooth loci. That is, a jaw with fewer preserved teeth, but at a similar or more advanced stage of eruption (e.g., DPC 22765 with dp1-4 and m1, 3-3-3-3-6 = 18/30 or 0.6), may have a

lower eruption ratio compared to a less mature jaw that has more preserved teeth (e.g., DPC 11684 with di1-2, dc, dp1-4, incompletely erupted m1 and m2 in crypt, 4-4-4-3-3-3-3-5-4 = 33/54 or 0.61). We therefore also quantified dental maturity using just p1-m3, as nearly all of our CT-scanned dentaries of *T. meyeri* and *S. boweni* could be coded for these cheek-tooth loci. In no case did a specimen with an eruption pattern indicative of immaturity (e.g., an incompletely erupted m1) exhibit a higher eruption ratio using p1-m3 than another with more fully erupted teeth, but fewer preserved loci.

To define "adult" jaw size based on samples that lack direct evidence on chronological age (as is nearly always the case in paleontology), we relied on evidence from tooth wear and eruption. That is, fully adult, "old" individuals generally have a completely erupted, permanent dentition, and in general also show substantial wear on at least some of their teeth. While lack of a fully erupted, permanent dentition does not guarantee that an individual is below adult body size and reproductively naive, especially in Afrotheria (Asher & Lehmann 2008; Asher & Olbricht 2009) and *Dasybus* (Ciancio et al. 2012), the converse is not true. That is, except for cases of pathology, it is likely that an individual showing fully erupted, permanent teeth with wear is older than another individual of the same species with unerupted and/or unworn teeth. Therefore, we calculated the median value of two measures of jaw length (posterior condyle to anterior symphysis and anterior coronoid to posterior symphysis, Fig. 1) for all dentally adult individuals of each species to define two values of "median adult size". For symphysis-condyle length in *P. capensis*, we used the median of 63.4mm among 13 individuals measured by Asher & Lehmann (2008); for posterior symphysis-anterior coronoid in other taxa, we used the median values for each species based on individuals with fully erupted,

lower third molars. As noted above, for *T. meyeri* this was based on five individuals measured using calipers; for other fossils we measured lengths using the "path" command in Drishti (Limaye 2012). Adult jaw sizes were then used to determine if, as previously observed in most afrotherians (Asher & Lehmann 2008; Asher & Olbricht 2009), dasypodids (Ciancio et al. 2012), and some ruminants and feliform carnivorans (Asher et al. 2009; Asher 2013), hyracoids attain adult jaw size prior to the complete eruption of their permanent teeth.

Eruption sequences and development

We collected data on dental eruption in extant primates, *Tupaia*, and afrotherians (Supplementary Datafile 1B, 1C), and combined our eruption sequences with data from Smith (2000), Godfrey et al. (2005), and Guthrie & Frost (2011). We excluded taxa when they lacked data for all loci (e.g., Smith 2000: fig. 15-1 for *Microcebus*, *Pithecia*, and *Cacajao*). In some cases it is difficult to distinguish between simultaneous eruption and lack of resolution. However, the first lower molar is generally the first permanent tooth to erupt, and its position in the sequence is clear even in cases of low resolution (e.g., *Tenrec* and *Tupaia*). Four taxa (*Macroscelides*, *Rhynchocyon*, *Callicebus*, and *Homo*) show presence of one or more antemolars simultaneously with the first molar, which we interpret to mean genuine early eruption of these loci. In contrast, the apparently simultaneous eruption of antemolars with m2 or m3 (e.g., apparent eruption of i3 and p2 with m3 in *Tupaia*) is more likely due to a sample too small to reveal the actual timing; we therefore regard these instances as cases of non-resolution and count loci as erupting before M2 or M3 only if they are resolved as doing so.

We identified a few cases of inconsistent eruption sequences: Guthrie & Frost

(2011) stated that M3 is the last locus to erupt in *Lemur catta*; however, our data (Supplementary Datafile 1C, 1D) and Smith (2000: fig. 15-1) support the interpretation that p2-4 erupt after m3, not before. Smith (2000: fig. 15-1) gave an incomplete eruption sequence for *Tarsius* (accounting for only two of the three premolars); we follow Guthrie and Frost (2011: table 5) instead. We also follow Guthrie and Frost (2011) for *Pan troglodytes* which is lumped into an "all apes" category by Smith (2000: fig. 15-1, who was in turn based on Schultz 1956).

We obtained data on gestation length and age at female sexual maturity from HAGR (<http://genomics.senescence.info>), which are unfortunately absent for dentally well-documented primates such as *Avahi* (Godfrey et al. 2005) and tenrecids such as *Oryzorictes* and *Potamogale* (Asher & Lehmann 2008). However, life history data are available for five (maturity) or six (gestation) genera in three high-level clades in Afrotheria (Hyracoidea, Macroscelididae, Tenrecinae; taxonomy follows Asher & Helgen 2010), and 18 genera in 10 high-level clades in Euarchontoglires (Tupaiaidae, Lemuridae, Tarsiidae, Aotidae, Cebinae, Pitheciinae, Cercopithecinae, Colobinae, Hylobatidae, and Homininae), as given in Supplementary Datafile 1E. We did not include additional afrotherian genera beyond hyracoids, tenrecids, and macroscelidids into our comparisons of eruption for several reasons. First, chrysochlorids exhibit variable and closely spaced eruption of several of their tooth loci, making inference of a precise eruption sequence difficult based on the rare and incomplete ontogenetic series available in museum collections. Living proboscideans and sirenians lack permanent antemolars (except for the tusk in elephantines and *Dugong*); proboscideans and manatees furthermore exhibit horizontal replacement of their molars and deciduous premolars; and dental homologies in orycteropodids are uncertain and, again, museum collections rarely contain specimens exhibiting

eruption and/or replacement.

In the cases where we can infer dental eruption sequence, comparisons of molars vs. antemolars can be made in several ways. We opted to add the number of teeth erupting with or before m1, plus the number before m2, divided by the species-typical number of teeth present in each dental quadrant. We used m1 and m2 because our four macroscelidid afrotherians lack an m3 (as do all macroscelidids except *E. brachyrhynchus* and *E. fuscipes*). For example, humans have one locus erupting at or before m1 and six before m2, summing to seven. Divided by the number present in each quadrant (eight), this gives an antemolar eruption value of 0.88, and enables comparison of taxa with varying dental formulae. If Schultz's Rule is generally accurate, then we would expect higher antemolar eruption values (i.e., more antemolars erupting prior to m1-2) to correlate with extended gestation times and later ages at maturity. We assessed significance of a given correlation coefficient for Afrotheria and Euarchontoglires using the degrees of freedom based on both number of sampled genera and (to account for the potential of phylogenetic autocorrelation; Felsenstein 1985) the smaller number of high-level clades within each, i.e., 3 clades (vs. 5 or 6 genera) in Afrotheria and 10 clades (vs. 18 genera) in Euarchontoglires.

RESULTS

Species definitions among fossil hyraxes

The hyracoids considered here (in order from smallest to largest tooth size) are *P. capensis*, *T. meyeri*, *S. bowni*, *T. domorictus*, *S. antiquum*, and *T. litholagus*. The two species of *Saghatherium* and *T. domorictus* are close in size, but of these three, we agree with Rasmussen and Gutierrez (2010: 133) that *S. antiquum* is the

largest (Fig. 2). Rasmussen and Gutierrez (2010) furthermore noted that *S. antiquum* does not occur at L-41, and that *S. bowni* and *S. antiquum* "represent two well-defined, cohesive species, possibly in an ancestor-descendent relationship, that occur in Egypt's latest Eocene and earliest Oligocene [see Bown et al. 1988], respectively."

The remaining hyracoid species considered here are readily distinguishable. Extant *Procavia* differs from all fossils in lacking an m3 hypoconulid, loss of two upper incisors and one lower incisor, loss of at least one anterior lower cheek tooth, and in exhibiting high-crowned cheek teeth, particularly on the molar talonids (Fig. 3). *T. meyeri* overlaps in size with *P. capensis* (Fig. 2), but differs from it in consistently having lower canines adjacent to p1, three upper and lower incisors, slightly larger molar hypocones and slightly smaller molar parastyles. *Sagatherium* is larger, and shows little overlap in lower m1 size with *Procavia* and *T. meyeri* (Fig. 2). It has lower molars with a distinctive buccal cingulid that are wide at the base of the crown (Fig. 3). *T. litholagus* molars are much longer, and slightly wider, than those of other taxa (Fig. 2).

Relatively well-preserved skulls with upper dentitions were available for two of the fossil taxa (*S. bowni* and *T. meyeri*) and are also easily distinguishable from each other and from living *Procavia* (Fig. 4). Compared to *Sagatherium*, upper cheek teeth of *T. meyeri* are smaller, more gracile, and have a much less pronounced postmetacrista-posthypocrista ridge forming the distal margin of each molar. This structure is particularly extensive on the M3 of *Sagatherium*, which gives this tooth considerably more occlusal area than M1 or M2 (Fig. 4). The molar parastyles of *T. meyeri* are present but also smaller than those of *S. bowni*. Parastyles on P1-4 of *T. meyeri* are relatively larger and similar in both taxa, but again *Sagatherium* can be

distinguished by virtue of its more conspicuous buccal cingula on both premolars and molars (Fig. 4). Deciduous upper premolars in *T. meyeri* and *S. bowni* are more molariform than their permanent replacements, due in part to their relatively larger hypocones, parastyles, and metacones. The parastyles on P1-3 of *T. meyeri* are slightly larger than those of P1-3 in *Saghattherium*. Crowns in both the upper and lower deciduous teeth are substantially lower in height than those of the permanent teeth of all hyracoids studied here.

Extant *P. capensis* has larger coefficients of variation ("CV" or standard deviation expressed as a percentage of the mean) for measurements of molar area than the fossil species represented in our sample by more than two specimens (Fig. 2). Based on measurements derived from CT scans, CV for *Procavia* m1 area is 14.6 (n=11) compared to 8.8 for *S. bowni* (n=11), 10.3 for *T. meyeri* (n=11), and 9.7 for *T. litholagus* (n=3). With a larger sample of fossil taxa derived from hand-caliper measurements, we recover similar CVs: 9.6 for *S. bowni* (n=25), 10.1 for *T. meyeri* (n=30), and 11.6 for *T. litholagus* (n=9). The lower variation in our fossil hyrax samples compared to *Procavia* may result from the fact that the above fossil species are from a single locality (Fayum L-41). Our sample of specimens of *S. antiquum* (from quarries F and B-2) and *T. domorictus* (from L-46) were insufficient to quantify their variation. As with any fossil site, there is likely to be at least some time-averaging, possibly greater than the century or so during which *P. capensis* was acquired into museum collections. On the other hand, our sample of extant *Procavia* covers a much wider geographic range, from South Africa to Cameroon to Ethiopia (Table S1).

Dental homologies in living procaviids

Prenatal, ontogenetic series of extant hyraxes reveal variably occurring, diminutive toothbuds that never fully mineralize or break the gums, but that can help establish tooth homologies (Hautier et al. 2016). Fetuses of *Procavia* and *Heterohyrax* generally show a mineralized but incompletely erupted upper dentition consisting of one incisor, from one to three small developing crowns, and four premolariform teeth (Fig. 5). In fetuses of *Heterohyrax* (e.g., USNM 181604, 181606), the upper M1 is generally not yet mineralized and there are four deciduous premolariforms, anterior to which are three small tooth buds close to the boundary of the maxilla and premaxilla (dC, dX, and dI2 in Fig. 5G and 5H). Assuming the posterior two of these toothbuds (dC and dX) are distinct loci in the maxilla, then M1 would be preceded by six maxillary teeth, which would deviate from the maximum number typically observed among living placental mammals (up to four premolars and one canine). Alternatively, the two small, posterior mineralization centers ("dC and dX" in Fig. 5G) could actually both comprise the dC, as our observations show that more posterior deciduous loci also show multiple mineralization centers early in development. It is also possible that "dX" corresponds to a vestigial dI3. However, its position at the anterior margin of the ossifying maxilla may disqualify this locus from being a posterior incisor.

Whatever the identity of this "dX" vestigial locus may be, we have consistently observed more than three maxillary teeth anterior to the dP4 in our sample of extant hyracoids (Fig. 5), contra the assessment of Lockett (1993: 279-280), quoted above. The anterior-most locus in the maxilla that erupts in juvenile specimens (Fig. 5E, 5J) is small with just one primary cusp and is anterior to four replaced, deciduous premolars (Fig. 5E). Moreover, the anterior-most, maxillary tooth that is replaced in *Procavia* (e.g., Fig. 4F) is molariform, with a hypocone, like the first premolar of

Thyrohyrax and *Saghatherium* and unlike the canine in these taxa (present simultaneously with P1; see Fig. 4A, 4D, 4E). Hence, while a deciduous canine may erupt and persist in some adults, it is not replaced, and our observations support Roche (1978), Fourie (1983) and Seiffert (2007) in regarding the permanent upper P1, not the canine, to persist in the permanent dentition of extant hyracoids.

Regarding the lower dentition, postnatal specimens of *Procavia* typically exhibit three or four replaced premolariforms posterior to the two lower incisors and anterior to the three molars (e.g., Figs. 3A, 6B). As noted above (Roche 1978), older specimens often lose the anterior-most premolariform, with little or no trace of the alveolus, leaving three premolars and three molars. In prenatal specimens, we have observed a lower dentition consisting of two deciduous incisors, a tiny deciduous rudiment of what may be the canine, followed by four deciduous premolars (Fig. 5B). The locus we tentatively identify as the lower deciduous canine generally becomes resorbed in older specimens, although we have observed rare specimens of *Dendrohyrax* (e.g., MNHN 1883-868) and *Heterohyrax* (e.g., RMCA 3637) in which this deciduous locus is erupted. We favor the canine identification due to the positional correspondence between upper and lowers (Fig. 5C). As with the upper dentition, we interpret the anterior-most locus among the four that are often present in extant hyracoids as the p1, not the canine.

Complicating matters is the fact that while the p1 locus in extant hyracoids appears to be replaced in at least some specimens (Fig. 6B), in others it is absent (e.g., ZMB 21849, UMZC H5101A, Fig. 9), and in yet others a lower dp1 may persist with no sign of a permanent replacement (Fig. 6D). Thus, as observed by Roche (1978) and coded by Seiffert (2007: character 18), specimens of *Procavia* may lack a p1 locus and exhibit just three loci (p2-4) between i2 and m1. When present, the dp1

is two-rooted with a premolariform crown (e.g., Fig. 6C, 6D). It is in some cases replaced by a one-rooted (Fig. 3A) or two-rooted (Fig. 6B) tooth with a higher crown with one main cusp and a smaller cusp immediately posterior to it. Dentaries of *Procavia* that show four loci between i2 and m1 (e.g., UMZC H4980J, UMZC H4980K, ZMB 21882, ZMB 21851; see Fig. 6) exhibit p1-4, not a canine followed by p2-4. Regardless of p1 replacement, results indicate that the permanent canines do not erupt in extant hyraxes. This supports the dental formula for fully grown members of this species used by Roche (1978), Fourie (1983), and Seiffert (2007).

Eruption sequences in hyracoids

In addition to an understanding of positional homology, a clear definition of "full eruption" is necessary to determine eruption sequence. We define full eruption when the enamel-dentine junction (EDJ) of a given tooth appears at the alveolar plane, following Asher & Lehmann (2008; but see alternatives below). In *Saghattherium* and *Thyrohyrax*, tooth homology is straightforward for all loci except for the third lower incisor. One specimen of *S. boweni* (DPC 17844) shows what we interpret to be a displaced left i1, with the lateral-most tine broken off but the other two intact and without wear (Fig. 7). It also shows a fragment of the anterior dentary, displaced from the rest of the jaw but with an intact right i2 and ?di3. We favor interpretation of the latter as di3 based on the presence of large alveoli (unfortunately with missing crowns) for i3 in other specimens of *S. boweni* (e.g., DPC 13282, 12048; Fig. 7), alveoli that would have held a larger permanent tooth than the single-rooted, short-crowned tooth evident in DPC 17844. One specimen of *T. meyeri* (DPC 17017) shows a similarly sized tooth in the i3 locus as that of DPC 17844, but this is missing the crown, and has furthermore been altered

taphonomically so as to result in slight CT artefacts (Fig. 7). This locus is nonetheless likely also a di3 based on its small root. The i3 of *Saghatherium antiquum* figured by Gheerbrant et al. (2007: fig. 2B) is small, but has a slightly larger crown than the tooth we identify as di3 in *S. bowni* (DPC 17844; Fig. 7).

To the extent that they are resolved, *Thyrohyrax meyeri* and *Saghatherium bowni* exhibit mutually consistent eruption sequences (Table 3; Supplementary Datafile 1D). Upper and lower M1 are the first permanent teeth to begin and complete their eruption. The growth series of the lower dentition for *T. meyeri* (Fig. 8) is more resolved than that of other fossil taxa, and shows m2 as the second permanent locus to erupt. This is followed by i2 and p1-2, then c and p3, then p4, then m3. Not enough specimens retain information on i1 or i3 eruption to fully document their placement in the sequence. In the lower dentition of *Saghatherium bowni*, m1 is again first, and at least i1-2 begin to erupt prior to any of the premolars (e.g., DPC 17844; Figs. 7, 9). The p1-3 loci mineralize prior to p4 (e.g., DPC 16527). *S. bowni* (DPC 24040) and *T. litholagus* (DPC 20624) also show a mineralized lower canine within its crypt prior to signs of any of the premolars. However, order of mineralization does not entirely correspond to eruption order, and there are too few specimens with intact incisors to specify their position in the sequence, beyond the fact that they erupt after m1 (DPC 17844, Fig. 7). In addition, it is probable but not certain that p1-3 in *Saghatherium* erupt after m2. One specimen of *S. bowni* (DPC 20509, Fig. 9) shows the posterior root of p1, erupted crowns of p2-3, dp4, and m1-2; mineralized m3 and p4 are still in their crypts. Wear on the m2 in this specimen is slightly more evident than on p2-3, and likely indicates that like *T. meyeri*, m2 erupts before p2 and p3.

The m1 is the first permanent lower tooth to fully erupt in *Procavia*. This is

followed by i2, i1, [p2-3], p1, [m2,p4], and finally m3 (with ties or ambiguity indicated by brackets). The indistinct eruption of m2 vs. p4 is based on slower appearance of the EDJ at the alveolar plane for the m2 in some specimens (e.g., UMZC H4981B, ZMB 21806), as noted above. Other specimens (e.g., ZMB 21849, UMZC H4980J, UMZC H5051A), show a dp4 in occlusion while m2 is nearly erupted. For the upper teeth, M1 is the first to approach full eruption; when its EDJ is close to the alveolar plane, the deciduous premolars are still in occlusion (e.g., ZMB 14148), and the permanent premolars are just beginning to mineralize (e.g., UMZC H4981E). However, at least one specimen (UMZC H4980K, Fig. 4) shows that the M1 EDJ may take some time to reach the alveolar plane, and that the EDJs of the permanent P1 and P2 reach it just before those of P3 and M1. Eruption at these loci is therefore close, but the upper M1 crown is larger than those of P1-3 and the EDJ of the latter more quickly reach the alveolar plane than the EDJ of M1. The timing of eruption in the upper P4 and M2 is similarly close; however, in this case the slightly larger M2 crown still erupts just prior to that of P4 (e.g., UMZC H4980J, H5051A). Therefore, as long as the definition of full dental eruption is when the EDJ reaches the alveolar plane, the sequence of eruption in the upper teeth of *Procavia* is [P1-2], [I1,P3,M1], M2, P4, M3. If, on the other hand, full eruption is defined as movement of the crown beyond the alveolar plane, with cusps beginning to occlude with the opposite tooth, then the upper sequence would be M1, I1, [P1-2],P3, M2, P4, M3 and the lower would be m1, i2, i1, [p2,p3], p1, m2, p4, m3.

Whichever definition for "full eruption" is used, there is a difference in sequence between Paleogene hyracoids and living *Procavia*. The lower p1-3 and i1-2 in *Procavia* erupt prior to m2, whereas in *T. meyeri* (DPC 13921, DPC 13299) m2 is fully erupted prior to i2 and the premolars. As noted above (based on DPC 20509),

this is likely also the case for *S. boweni*. As shown in Fig. 10, individual specimens of other extinct hyracoid genera, including *Microhyrax* (UM-HGL 50-102), *Bunohyrax* (AMNH 13336), *Megalohyrax* (AMNH 13345), and *Pachyhyrax* (DPC 4876), all show the lower m2 at or near full eruption, simultaneously with the permanent premolars still in their crypts. The advanced eruption of premolars in *Procavia* is also evident in its upper dentition. UMZC H4980K (Fig. 4) shows an upper M1 EDJ that is still occluded under the maxilla, after some or all of the EDJs of P1-3 are already exposed. In contrast, *S. boweni* (DPC 12061, Fig. 4) shows a nearly erupted and slightly worn M1 with dC and dP1-4 with slightly more wear, and an M2 beginning to erupt, implying (but not guaranteeing) that some or all of its permanent premolars will not erupt until after M1 or even M2. Otherwise, the sequence for the upper teeth in fossils is not as well resolved as for the lowers, beyond the shared eruption of the last molar (M3) as the final permanent tooth to erupt in all hyracoids.

Life history and eruption

While the absolute dates of eruption are variable in previous studies (as noted in the Introduction), our data on eruption sequences in *Procavia* agree with those from Roche (1978), Fairall (1980), and Fourie (1983) that several antemolar loci erupt prior to m2, and all of them erupt prior to m3. This contrasts with the eruption of most antemolars after m2 in *Thyrohyrax* and *Saghatherium*. Our sample of tenrecines resembles fossil hyracoids in that m1 and m2 are the first two permanent teeth to erupt, prior to any antemolars. Macroscelidids are more variable, ranging from *Petrodromus tetradactylus* and *Petrosaltator rozeti* (formerly *Elephantulus rozeti*; see Dumbacher 2016) in which p1 erupts before m1 and m2, to *Rhynchocyon* in which i1 and p1 erupt with or before m1 and i2 erupts before m2, and

Macroscelides in which p1 erupts before m1 and i3 and the canine erupts prior to m2. Among afrotherians, neither age at maturity (from ca. 40 days in macroscelidids to 190 days in *Setifer* and *Tenrec*) nor gestation time (ca. 42-76 days in macroscelidids to ca. 56 days in *Setifer* and *Tenrec*) show a positive correlation with the number of teeth erupting at or before m1 and m2 (Fig. 12). *Procavia* is an outlier for afrotherians. It has a very long gestation time (seven months) for its body size, a relatively late age at maturity (ca. 500 days), and it has the highest number of teeth erupting at or before m1 and m2 (i.e., six, giving an eruption value of 0.67 when scaled by the nine teeth present in each half of its jaw). Nonetheless, considering *Procavia* along with tenrecines and macroscelidids, a best fit line of either age at maturity or gestation time to the sum of teeth erupting at or before m1 and m2 is not statistically significant (Fig. 12).

In fact, if *Procavia* is excluded as an outlier, and because of a substantial difference in age at female maturity between tenrecines compared to macroscelidids, there is actually a slightly negative correlation between the sum of teeth erupting prior to m1 and m2 and the age at maturity. Tenrecines mature later but erupt all molars prior to antemolars; macroscelidids mature more quickly but erupt p1 and/or some incisors at or before m1 and m2. These taxa do not show a comparable difference in gestation time (tenrecines fall within the range observed among macroscelidids); therefore, without *Procavia*, this life history variable does not significantly correlate with the sum of teeth erupting prior to m1 and m2.

A final qualification concerning potential correlations between eruption patterns and life history concerns the homology of the macroscelidid p1. Based on histological data, Kindahl (1967) proposed that the p1 locus in macroscelidids, generally regarded as the first permanent tooth to erupt, is actually a retained

deciduous tooth. It does not show a molariform or dorso-ventrally narrow crown, features which characterize deciduous teeth in general. Nonetheless, Kindahl outlined the histological case that a replacement toothbud at the p1 is absent, and (unlike the histological data presented by Lockett 1993) no data yet available to us can refute this. We therefore also quantified eruption patterns in macroscelidids assuming that the p1 locus is deciduous, meaning in practice that there are nine permanent teeth in each half of the macroscelidid jaw, not 10, and that only some incisors and/or canine erupt at or before m1 and m2, not the "p1". This treatment does not change our overall result that, among afrotherians, there is no positive correlation between an increased number of teeth erupting prior to the molars and either gestation length or age at maturity (Fig. 12; Table 4).

For primates and *Tupaia*, there is generally a significant correlation between both gestation length and age at maturity with the sum of teeth that erupt prior to m1 and m2, depending on assumptions concerning the degrees of freedom and inclusion of the outlier *Homo*. Assuming that each sampled genus is an independent data point, and including *Homo*, the sum of teeth erupting at or before m1 and m2 shows a significant, positive correlation with both gestation length and age at female maturity (Fig. 12; Table 4). In both cases, the significance remains with a reduced number of degrees of freedom (using 13 high-level clades of primates and *Tupaia*, rather than 18 genera). Excluding *Homo* (an outlier for both gestation length and age at maturity), there is still a significant, positive correlation with gestation length assuming each sampled genus is an independent data point. However, the correlation with age at maturity is no longer significant, nor is the correlation with gestation length, with degrees of freedom derived from 13 high-level clades rather than 18 genera (Table 4).

DISCUSSION

Growth and eruption in hyracoids

Changes in tooth position---The relative placement of teeth in both the maxilla and mandible of *Procavia* is not static during growth. While dental replacement is vertical as in most mammals, i.e., from below in the mandible and above in the maxilla, the positions of molar and premolar loci relative to other parts of the skull change during growth. An extreme form of tooth migration during growth is the "horizontal" tooth replacement observed in manatees (Domning & Hayek 1984), living and some fossil proboscideans (Shoshani et al. 2006), macropodids (Sanson 1980), and bathyergid rodents (Gomes-Rodriguez et al. 2011). As new teeth erupt in these taxa, they do so from behind and push more anterior loci forward. Of course every mammal has to make room in its jaw for erupting teeth, and changes to the proportions of the skull in mammals in response to dental eruption are known in several cases (Godfrey et al. 2005).

In *Procavia*, the relative positions of M1 and the root of the maxillary zygoma change during growth (Fig. 9). When both upper and lower M1 loci are erupting (e.g., UMZC H4981D), the root of the maxillary zygoma is entirely anterior to M1. By the time the upper & lower M1s are erupted and the M2 apices have broken the alveolar plane (UMZC H4980J), the zygoma is posterior to M1. These relative positions do not greatly change as the permanent P4 erupts (UMZC H5051A), but when the EDJ of M2 and lower m3 is visible above the alveolar plane, and M3 is still incompletely erupted (UMZC H5101A), the zygoma is posterior to most of M2 (Fig. 9), as it is in at least some specimens with fully erupted upper and lower M3s (UMZC H5081B). A few specimens of similar size and with a fully erupted dentition show the zygoma

extending slightly posterior to the anterior root of M3 (e.g., ZMB 11743).

Similarly, among our youngest postnatal specimens of *Procavia*, *Sagatherium*, and *Thyrohyrax*, the anterior margin of the coronoid process is immediately lateral to the newly erupted m1 (Figs. 8, 9). As the jaw increases in size, and as more teeth erupt, the jaw elongates and the anterior coronoid moves posteriorly relative to the m1. Both m2 and m3 appear to erupt just medial to the anterior margin of the coronoid; eventually the hypoconulid of the elongate m3 in *Sagatherium* (Fig. 9) and *Thyrohyrax* (Fig. 8) is exposed just anterior to the coronoid in our largest and presumably oldest specimens. The m3 of *Procavia* lacks a hypoconulid, but is still visible anteromedial to the coronoid process (Fig. 9).

Delayed eruption in hyracoids?---Asher & Lehmann (2008) suggested that morphologically disparate afrotherians such as macroscelidids, trichechids, tenrecids, chrysochlorids, proboscideans, and hyracoids shared with each other late eruption of the permanent dentition. This was based partly on known chronologies of dental eruption (as in manatees, elephants, hyraxes, and sengis), and on the observation that members of these species may attain adult size with an incompletely erupted dentition (Leche 1907; Asher & Olbricht 2009). Ciancio et al. (2012) noted that *Dasypus* (the only living diphyodont genus of Xenarthra) also reaches adult jaw length while possessing only a fraction of its permanent dentition. The chronology of molar eruption (especially M3) among *Procavia* individuals of known age (e.g., Roche 1978; Fourie 1983) demonstrates that sexual maturity (ca. 16 months) long predates full dental eruption (ca. 5 years). Focusing on the cheek teeth, Asher & Lehmann (2008: fig. 2) furthermore noted that eruption of the upper and lower P4, M2, and M3 in *Procavia* generally occurs after the individual has reached adult body size. Data for the entire dentition indicates that while true for

these loci, eruption at others (incisors and anterior premolars) does overlap with growth, and is not delayed until after adult body size is reached, unlike macroscelideans, chrysochlorids, and some tenrecids. Overall, and as a proportion of median adult jaw length, dentally immature individuals of *Procavia*, *Saghattherium*, and *Thyrohyrax* (Fig. 11) are more often below adult size than other afrotherians and *Dasypus*. Moreover, while individuals of *Procavia* can exhibit symphysis-condyle lengths (Fig 12, "SC") at or over 95% that of the median value for adults despite lacking a fully erupted upper and lower P4, M2, and M3 (e.g., UMZC H4980J, see Fig. 11 and Asher & Lehmann 2008), they are under 95% adult posterior symphysis-anterior coronoid lengths (Fig. 1, "SAC"), as are dentally immature specimens of *S. bowni* and *T. meyeri*. The most any of the dentally immature fossils (with m3 either unmineralized or entirely in its crypt) in our sample approximate adult size is a specimen of *T. meyeri* (DPC 13921), which at 82% of the adult SAC length (Figs. 1, 11) has dp3, dp4, and an m3 still in its crypt.

Eruption chronology---Previous studies of dental eruption in hyracoids (Roche 1978; Fairall 1980; Fourie 1983) gave variable results in terms of absolute timing (Table 1), and there are evidently differences in eruption among individuals that may be influenced by diet (e.g., the care regime for captive individuals described by Fairall, 1980) and geography (e.g., Levantine vs. South African *Procavia*). Furthermore, eruption variability may arise due to pathology (e.g., a peg-like left m1 in *Procavia* UMZC H5081B) and to the fact that not all past investigators have defined "full eruption" in the same way. Nonetheless, our observations on several dozen individual jaws of the extant *P. capensis*, and of CT scans of 41 individuals of *Thyrohyrax* and *Saghattherium*, reveal a consistent pattern of eruption for all hyracoids observed so far. Namely, the upper and lower M1/m1 is always the first

permanent locus to break the alveolar plane and enter into occlusion (although in *Procavia* the upper M1 is not always the first upper EDJ to reach the alveolar plane). The lower p4 is always the last replaced locus to erupt, and the remaining molars erupt in anterior-posterior order, with M3 as the last permanent tooth to erupt.

The differences given by past investigators concerning the absolute chronology of eruption may be substantial (Table 1), and as noted above are likely due at least in part to how eruption is defined. Data on eruption timing from Fairall (1980) are the most discrepant (Table 1). Given his own acknowledgment of ambiguity (as described in the Introduction) his data on absolute timing are not comparable with those of other authors and are therefore not considered further. Asher & Lehmann (2008: supplementary data #2) coded "full eruption" as binary: a given tooth locus was either erupted (EDJ at alveolar plane) or not. Fourie (1983: table 17) gave three categories for premolars: deciduous, replacing, and permanent. For molars, he defined six: visible in crypt, mid-eruption, nearly level, level, enamel-cementum boundary partly visible (ECP, which we interpret as just prior to appearance of enamel-dentine junction, or EDJ), and fully erupted. Given our data on *Procavia* eruption (see Results), it is evident that his category "permanent" for premolars encompasses several stages similar to his categories "level", "ECP", and "fully erupted" for molars. Moreover, his age category "9-12" months shows deciduous teeth in the canine and premolar loci; these loci all change to permanent in his "13-16" month age category. This masks several differences in the order of premolar eruption, in particular that the upper and lower P4 loci erupt after the other antemolars. If there were variation (e.g., p4 erupting before p2-3 in some individuals but after in others), we would expect to see at least some specimens with p4 in occlusion while p2-3 are erupting and/or in their crypts. Instead, when specimens of

Procavia have an erupted p4, they have an erupted p2-3, and conversely when they lack a fully erupted p2-3, they lack a fully erupted p4. The same is true in *Thyrohyrax* and *Sagatherium*. Thus, when premolar loci fall within the same ten- (Roche 1978) or two- (Fourie 1983) month age-bins, this does not imply simultaneous eruption, but simply means that such age-categories are not finely-grained enough to pick up what is in fact a consistently later-erupting p4 compared to other premolars.

In contrast to the consistently later eruption of p4 relative to p2 and p3, p4 and m2 erupt closer in time and may show variation across individuals, depending on how "full eruption" is defined. As just noted, Fourie's (1983) criteria were more finely graded than those of Asher & Lehmann (2008); he accurately reported the initial eruption of the M2 beyond the alveolar plane in a time bin (24-33 months) after that of the antemolars (12-15 months). However, due to its size, the EDJ of M2 may not reach the alveolar plane until the tooth has been in occlusion for some time, after which point the EDJ of P4 may have reached the alveolar plane. On this basis, Asher & Lehmann (2008) reported two specimens (UMZC H4981B, ZMB 21806) in which the lower m2 was not fully erupted, but the p4 was. Had the criteria for "full eruption" been oriented around the initiation of occlusion, rather than appearance of the EDJ, then these specimens would have been categorized differently, with p4 erupting after m2. In general, several specimens exhibit a functional dp4 while the m2 is already in wear (e.g., ZMB 21849, UMZC H4980J), whereas we have never observed an m2 within its crypt while the p4 is in functional occlusion. Hence, these two specimens do not contradict the general observation that m2 initiates and comes close to finishing eruption prior to p4.

Schultz's Rule---By noting correlations between life history and eruption patterns, Schultz (1960; see also Smith 2000; Godfrey et al. 2005; Schwartz 2012)

articulated a causal mechanism: species with an extended period of juvenile development (leading to later ages at maturity) and extended gestation times need a dental battery to last longer compared to those that mature quickly with short gestation times. Accordingly, antemolars erupt and are functional while at least some of the molars are still in their crypts, in theory waiting for what might be a period of substantial use after the antemolars become worn. If this were generally true, we would expect that species with longer gestations and longer times to reach maturity would exhibit more teeth erupting prior to their molars. This expectation is somewhat supported by data on primates and *Tupaia*, but not afrotherians (Fig. 12).

Proboscideans are the longest-lived afrotherians, with a lifespan and period of juvenile dependency comparable to humans and the longest gestation time of any mammal. Yet rather than change the eruption timing of the permanent antemolars relative to their molars, they have lost their antemolar replacement teeth (except for the tusk, or I2) altogether. Their three deciduous premolars and three molars erupt over an exceptionally long period of time (approaching 40 years; Laws 1968).

Elephantine teeth persist due more to their extremely high and long crowns rather than to any dependence on a permanent antemolar generation (which is lacking).

Manatees (trichechids) also lack late replacement of antemolars, shedding their antemolars long before sexual maturity (Domning & Hayek 1984). Unlike anthropoid primates, they do not accelerate eruption of permanent antemolars relative to molars, and unlike elephantines do not increase molar crown height and length. They do resemble elephantines in exhibiting horizontal tooth replacement without vertically replaced, permanent premolars, but posteriorly erupt many dozens of molariforms in each jaw quadrant that continually migrate forwards over an animal's lifespan (Domning & Hayek 1984).

Some non-primate groups in which aspects of Schultz's Rule has been tested so far appear to lack correlations of late-erupting posterior molars with life history variables such as longevity, maturity, and age at weaning (Veitschegger et al. 2016; Geiger et al. 2016; these studies did not separately investigate gestation length). In other instances such correlations do exist (Smith 2000; Jordana et al. 2013). Moreover, Godfrey et al. (2005) demonstrated that the primates *Avahi* and *Lepilemur* vary in the opposite direction to that predicted by Schultz's Rule, as did Guthrie and Frost (2011) for *Tarsius*. These results do not necessarily mean that Schultz's Rule is wrong, and within certain clades it may yet prove to be a "rule" (e.g., anthropoid primates). However, there are clearly multiple ways by which mammals have evolved to extend the lifespan of their functional dentitions, such as erupting a quasi-unlimited battery of molars (manatees) or greatly increasing crown height and length (elephants). Both are adaptations that circumvent the particular strategy evident in at least some primates as noted by Schultz (1960), i.e., to erupt more antemolars prior to molars and thereby extend dental functionality over a longer lifespan.

Modern hyracoids resemble anthropoid primates in having a long gestation length (but not a particularly late age at maturity) and fairly long lifespan for their body size, and in having more antemolars that erupt prior to molars compared to other, similarly-sized mammals. It is therefore tempting to consider what the implications for life-history might be for fossil hyracoids, given their different pattern of dental eruption compared to the extant *Procavia*. Focusing on the better-resolved lower dentition (Table 3), *T. meyeri* erupts only m1 prior to m2, and m3 is the last tooth to erupt. Hence, there are ten teeth prior to m3, one prior to m2, and none prior to m1. We have insufficient data to infer the sequence for the incisors of *Saghatherium*, beyond the fact that they erupt after m1. However, as previously

noted, all fossil hyracoids examined so far differ from *Procavia* in showing eruption of premolars after m2. Hence, our data indicate that all fossil hyracoids have fewer teeth erupting before their molars than extant *P. capensis*. Therefore, according to Schultz's Rule, we would expect the fossil hyracoids to exhibit a slightly "faster" development compared to *P. capensis*, i.e., faster growth and a correspondingly shorter time until size at maturity.

While we cannot yet directly test these predictions here, it would in theory be possible to do so. Fourie (1983: figs 40-43) showed that cementum growth annuli are evident in the tooth roots of *P. capensis*, and that they correlate well with known ages. He obtained thin slices of dental tissues by destructive sampling, a technique that is impractical for the unique and well-preserved fossil specimens documented here. Our microCT scans were between 16 and 64 μ m voxel size (Table S1), insufficient to reveal details such as growth lines within enamel, dentine, and cementum. Possibly synchrotron tomography would enable greater resolution without the need to disassemble or damage specimens. Should information on cementum annuli be forthcoming and yield approximate ages for individual fossils, and if Schultz's Rule applies to hyracoids (even though our data so far indicate that it is not generally applicable among afrotherians), we would make the following predictions: *Thyrohyrax meyeri* should reach an asymptote of adult size at a slightly younger age compared to the living *Procavia* (Fig. S1). We might also expect that the age at which all permanent teeth are erupted and show wear would similarly be lower than that observed in *Procavia*. *T. meyeri* evidently has an osteological signature of secondary sexual characteristics (i.e., mandibular resonating chamber in males, see DeBlieux et al. 2006). As for attainment of adult size, full development of this structure (assuming it correlates with maturation) should take place earlier compared

to age at sexual maturity in extant *P. capensis*.

Another potential correlate of eruption timing is crown height, as outlined by Böhmer et al. (2016) among rhinocerotids and Gomes-Rodriguez et al. (2017) among endemic South American ungulates. Specifically, rhinocerotids with hypsodont (i.e., high-crowned) cheek teeth erupt p2-3 before m2, whereas rhinocerotids with brachydont (i.e., low-crowned) cheek teeth erupt p2-3 after the m2. Among notungulates, the pattern entails p4 and m3, rather than p2-3 and m2, and is reversed: species with low-crowned cheek teeth tended to erupt premolars before M3; notungulates with high crowned teeth erupted P4 with M3; and notungulates with open-rooted, ever-growing teeth erupted P4 after M3.

Our sample of hyracoids lacks species with ever-growing cheek teeth, but does have a mix of high- and low-crowned species, notably *Procavia* which exhibits substantially higher crowned cheek teeth than either *Thyrohyrax* or *Sagatherium* (Fig. 3). While m3 is the last locus to erupt in all of these species, high-crowned *Procavia*, like rhinocerotids, shows earlier eruption of premolars relative to m2; in low-crowned *Sagatherium* and *Thyrohyrax* premolars erupt after m2. We cannot yet say if or how crown height might be causally linked to eruption timing, beyond the trivial observation that high crowns would be expected to take longer to erupt given that there is more dental tissue to lift above the gum line. Moreover, although we too observe a correlation, the overall pattern of eruption timing in *Procavia* (and rhinocerotids as documented by Böhmer et al., 2016) differs from that observed in notungulates. Gomes-Rodriguez et al. (2017) describe high-crowned notungulate premolars erupting with or after m3, whereas we observe high-crowned *Procavia* premolars erupting before m2 and m3.

Much of the preceding is admittedly speculative and insufficient to infer

specific, causal mechanisms that may be relevant to explain patterns of eruption timing in mammals, particularly given the known exceptions to Schultz's "Rule" (Godfrey et al. 2005; Guthrie & Frost 2011) and the fact that it has not yet been demonstrated outside of primates (cf. our Fig. 12, Veitschegger et al. 2016, and Geiger et al. 2016). Nonetheless, a full exploration of this topic, integrating data on eruption, growth, crown height, life history, and phylogenetic relatedness across mammals, holds substantial promise to shed light on aspects of the biology of long-extinct taxa that would otherwise remain unknown.

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FIGURE CAPTIONS

FIGURE 1. Hyracoid jaws showing accepted dental homologies and metrics used to compare growth patterns in living (*Procavia capensis*, UMZC H4981F, top) and fossil (*Thyrohyrax meyeri*, DPC 17675, bottom) specimens. Measurements are maximum length of 1) M1 and 2) m1, maximum width of 3) M1 and 4) m1, 5) distance between anterior margin of coronoid and posterior margin of symphysis (or “**SAC**”), and 6, distance between posterior margin of condyle and anterior margin of symphysis (or “**SC**”). Scale bars = 10mm. [page width]

FIGURE 2. Comparisons of **A**) first lower molar length (Y-axis) and width (X-axis) in mm. Squares = *P. capensis*, X = *T. meyeri*, + = *T. litholagus*, inverted triangle = *T. domorictus*, triangle = *S. boweni*, diamond = *S. antiquum*. **B**) lower molar area (m1 length X m1 width) across taxa. [column width]

FIGURE 3. Occlusal and buccal views of teeth & jaws of *P. capensis* (**A**, UMZC H.5051.A), *T. meyeri* (**B**, DPC 20777), *S. boweni* (**C**, DPC 12048), and *T. domorictus* (**D**, DPC 4057, image reversed). All scale bars = 10mm. [page width]

FIGURE 4. Occlusal and buccal views of upper dentition morphology in *T. meyeri* (**A**, DPC 15587; **B**, DPC 23087), *P. capensis* (**C**, UMZC H.5081.B, **F**, UMZC H.4980.K), and *S. boweni* (**D**, DPC 11548; **E**, DPC 12061). Scale bars = 10mm. [page width]

FIGURE 5. CT reconstructed scans of the developing skull and teeth in *Procavia* (left column) and *Heterohyrax* (right column), as follows: **A**, *Procavia capensis* (ZMB A1.19), skull length (SL)=32.1mm; **B**, *Procavia capensis* (ZMB 12), SL=33.4mm; **C**,

Procavia capensis (ZMB 10A), SL=39.91mm; **D**, *Procavia capensis* (MNHN CG 1981-994), SL=49mm; **E**, *Procavia capensis* (UM 076N), SL=71mm; **F**, *Heterohyrax brucei* (USNM 1639), SL=32.26mm; **G**, *Heterohyrax brucei* (USNM 181606), SL=37.6mm; **H**, *Heterohyrax brucei* (USNM 181604), SL=39.4mm; **I**, *Heterohyrax brucei* (USNM 576173), SL=43.3mm; **J**, *Heterohyrax brucei* (MNHN CG 1956-723), SL=46.3mm. Upper deciduous teeth are blue; lower deciduous teeth are green; upper permanent teeth are pink; lower permanent teeth are blue. **d** stands for deciduous teeth; **i**, **c**, **pm**, and **m** stand for lower incisors, canines, premolars, and molars (respectively). **I**, **C**, **P**, and **M** stand for upper teeth. **dX** represents an extra mineralization center located in front of the dC. dl2 and dc correspond to vestigial upper and lower teeth (respectively); these loci are absent in adults. [2/3 page width]

FIGURE 6. Occurrences of the permanent (**A**, UMZC H4980J; **B**, ZMB 11743) and deciduous (**C**, ZMB 21851; **D**, UMZC H4980K) first premolar in *P. capensis*. [column width]

FIGURE 7. Incisor morphology and homologies in *Saghattherium* (top, middle, and bottom right) and *Thyrohyrax* (bottom left). [page width]

FIGURE 8. Growth series in jaws of *Thyrohyrax meyeri*. Narrowly dotted line is through middle of m1; widely dotted line is through anterior margin of coronoid process. [column width]

FIGURE 9. Growth series of *Procavia capensis* (skulls, right) and *Saghattherium boweni* (jaws, left). Narrowly dotted line is through middle of m1; widely dotted line is

through anterior margin of coronoid process. [2/3 page width]

FIGURE 10. Jaws of *Microhyrax* (**A**, HGL 50-102), *Megalohyrax* (**B**, AMNH 13345), and *Bunohyrax* (**C**, AMNH 13336), all showing erupted or near-erupted lower m2 simultaneously with unerupted p1-4. [2/3 page width]

FIGURE 11. Scatterplot of the proportion of fully erupted, permanent teeth (X-axis) in *P. capensis* (black circles), *S. bowni* (dark gray triangles) and *T. meyeri* (light gray pluses) by jaw length expressed as the proportion of the median symphysis-anterior coronoid length (**SAC** in Fig. 1) among specimens with fully erupted lower m3 (Y-axis). DPC 13921 is the largest, observed specimen of *T. meyeri* retaining deciduous premolars. [column width]

FIGURE 12. Sum of teeth in afrotherians (triangles) and euarchontoglires (circles) erupting at/before m1-2 divided by the number of permanent teeth in each jaw half (Y axis) by gestation length (left X axis) and maturity (right Y axis). [page width]

TABLE 1. Age at eruption of permanent teeth in *Procavia capensis* in months given by previous authors. Note that Roche (1978:99-101) gives precise eruption timing only for the upper dentition, and Steyn & Hanks (1983: table 1) only for the molars. Fourie's (1983: table 17) observation of an erupting molar with an exposed enamel-dentine junction is interpreted as equivalent to completely erupted. "X" corresponds to each author's interpretation of a missing tooth locus.

uppers	I1	I2	C	P1	P2	P3	P4	M1	M2	M3
Roche	9-12		X	14-24	14-24	14-24	14-24	12-14	25	68-81
1978										
Fairall	10-12		X	10-12	10-12	12-15	12-15	2-8	15-24	24-36
1980										
Fourie	12-13		X	12-13	12-13	12-13	12-13	13-16	24-33	60-69
1983										
Steyn &								8-10	17-19	60
Hanks										
1983										
lowers	i1	i2	c	p1	p2	p3	p4	m1	m2	m3
Roche			X							
1978										
Fairall	10-12	10-12	X	10-12	10-12	12-15	X	2	10-12	15-24
1980										
Fourie	12-13	12-13	X	12-13	12-13	12-13	12-13	9-12	20-21	48-57
1983										
Steyn &								8-10	16	43
Hanks										
1983										

TABLE 2. Acronyms for museum collections used in this study.

BMNH = the Natural History Museum, London;

CBC = Cambridge Biotomography Centre;

DPC = Duke Lemur Center, Division of Fossil Primates, Durham;

ISEM = Institut des Sciences de l'Evolution de Montpellier;

MNHN = Museum Nacional d'Histoire Naturelle, Paris;

RMCA = Royal Museum for Central Africa, Tervuren

RSA = Republic of South Africa;

UM = Université Montpellier

UM-HGL = Université Montpellier, Hammada Gour Lazib collection

UMZC = University Museum of Zoology, Cambridge;

USNM United States National Museum, Washington DC;

ZMB = Zoologisches Museum Berlin (Museum für Naturkunde), Germany.

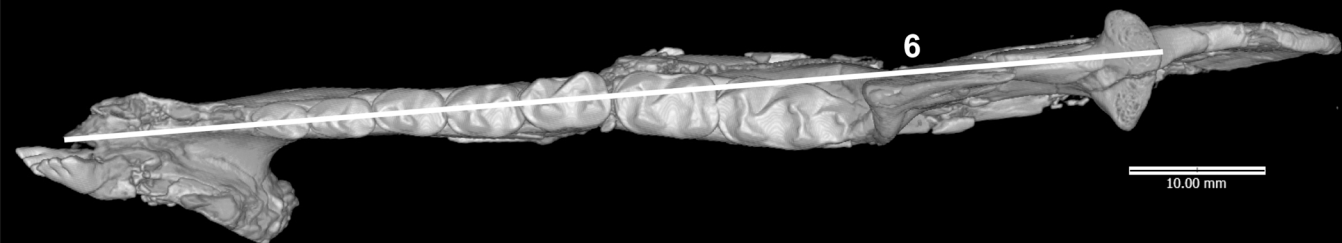
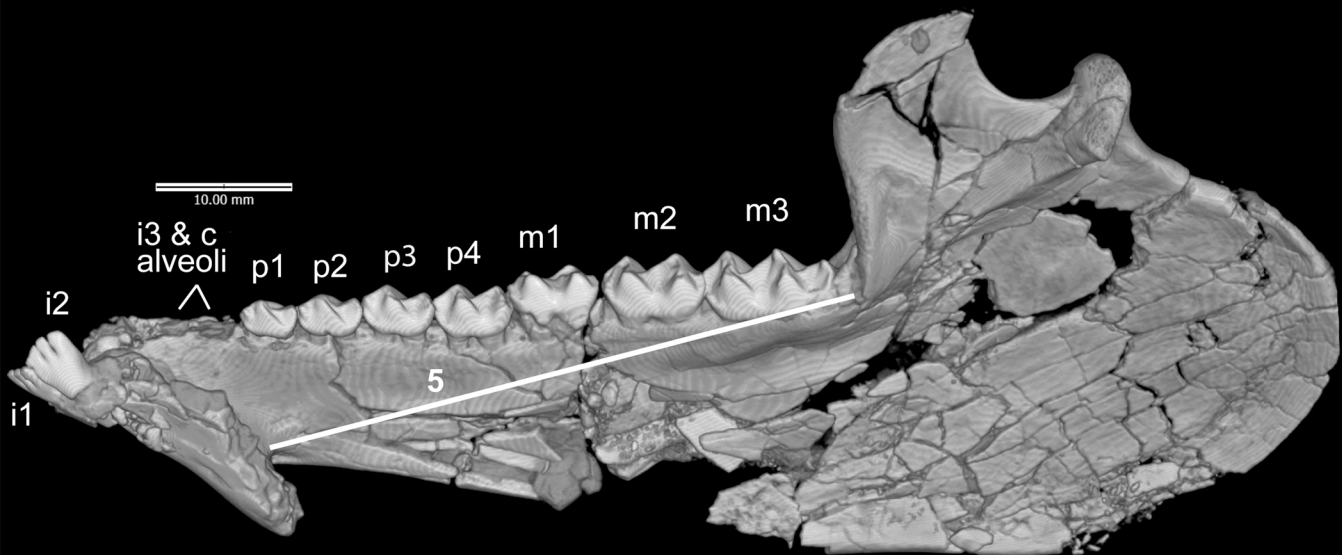
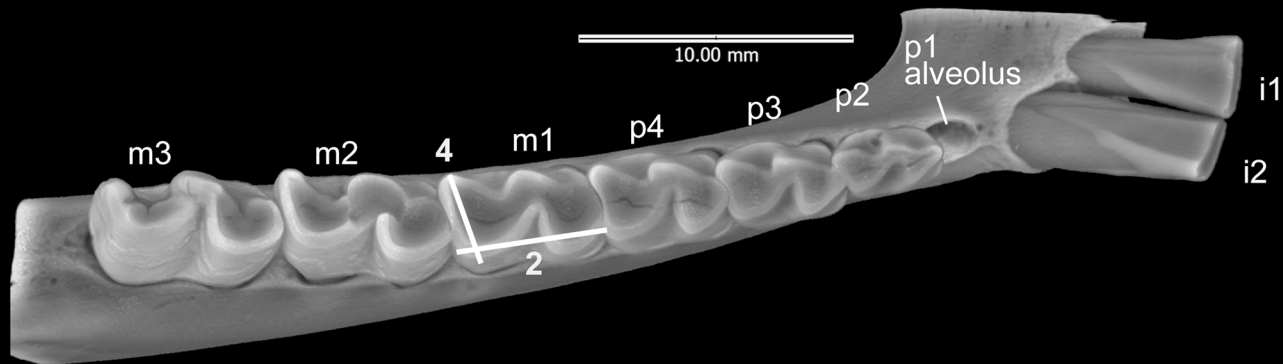
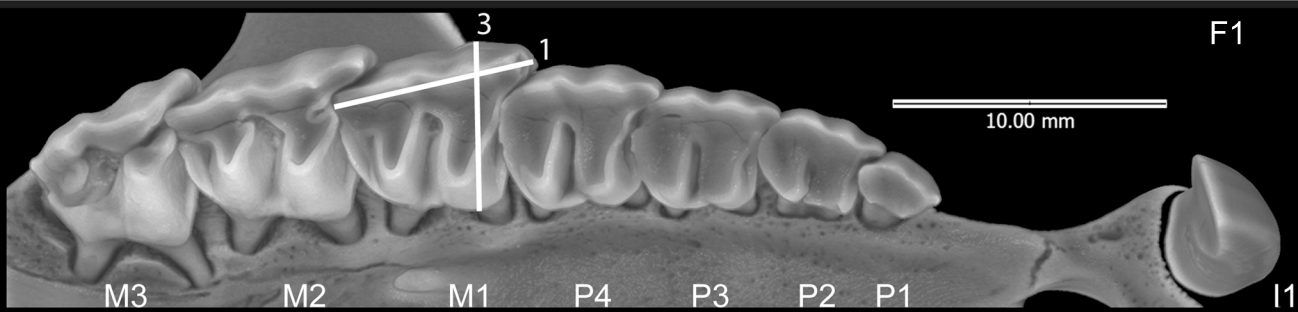
TABLE 3. Eruption sequences in hyracoids. Upper and lowercase I, C, P, and M refer to upper and lower incisors, canines, premolars, and molars, respectively. Brackets indicate either ambiguity or simultaneous eruption. Intact incisors in *S. bowni* specimens with erupting teeth are not preserved frequently enough to infer their sequence, except that they erupt after the lower m1 (DPC 17844). *P. capensis* shows higher cheek tooth crowns than either *T. meyeri* or *S. bowni*. *T. meyeri* DPC 13921 shows that i2 is still in crypt with an erupted m2. We interpret an *S. bowni* specimen (DPC 17844) as likely exhibiting a ?di3 still in place with a fully erupted m1.

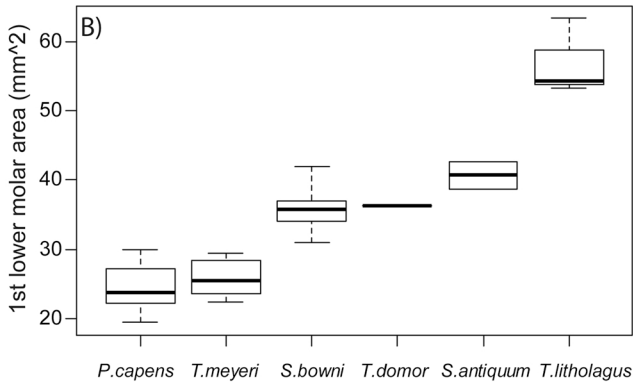
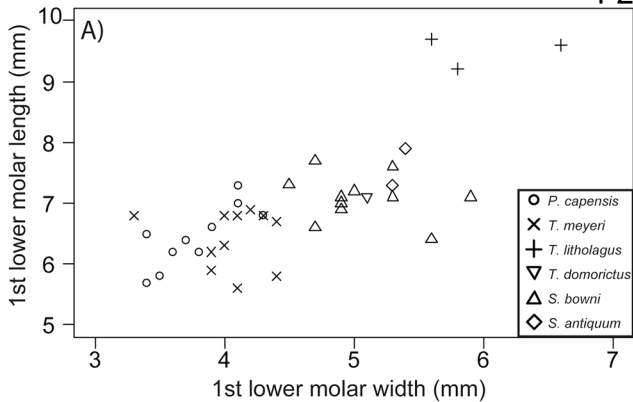
Lower dentition eruption sequence										
<i>P. capensis</i>	m1	i2	i1	[p2,p3]	p1	[m2,p4]				m3
<i>T. meyeri</i>	m1					m2	[i2,p1,p2]	[c,p3]	p4,?i3	m3
<i>S. bowni</i>	m1					m2	[p1,p2,p3]		p4	m3
<i>P.cap</i>	m1	[i,p]				m2				m3
<i>Fourie</i>										

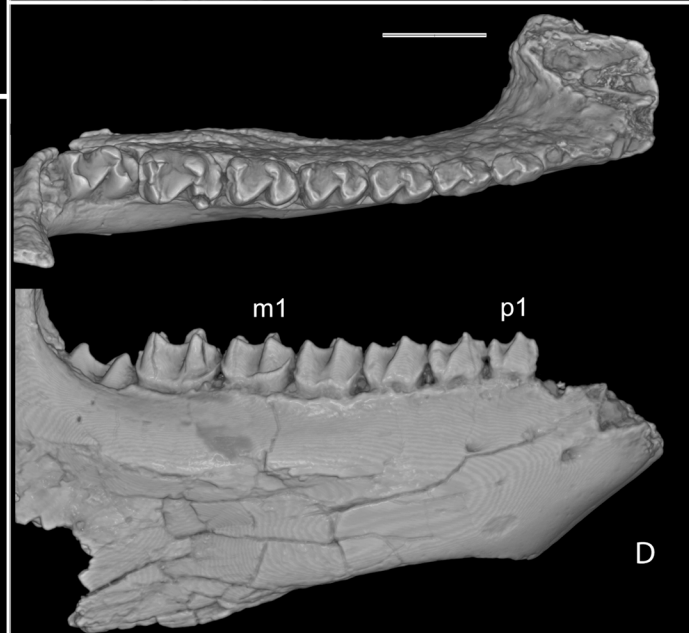
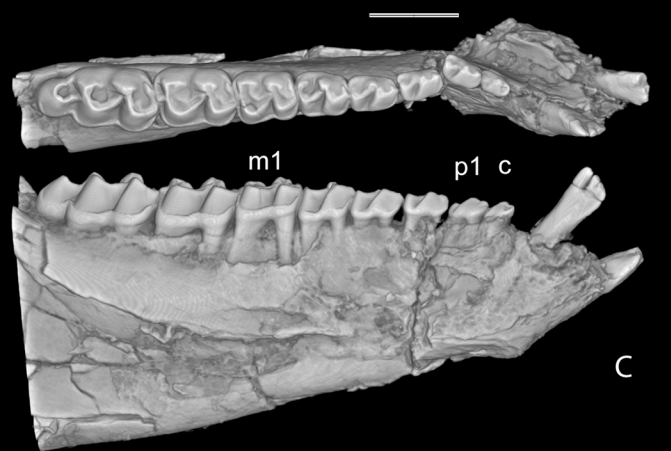
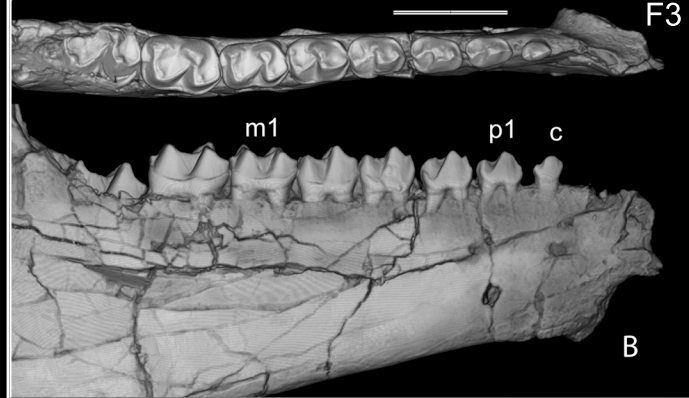
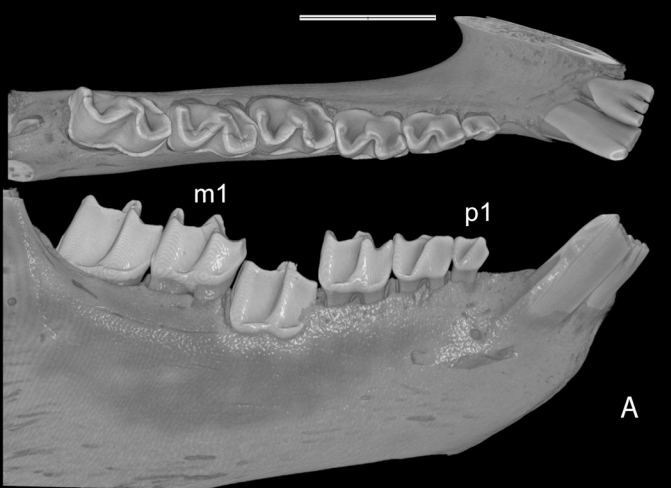
Upper dentition eruption sequence						
<i>P. capensis</i>		[P1,P2]	[M1,I1,P3]		M2	P4 M3
<i>T. meyeri</i>			M1			[M2,C,P1-4,M3]
<i>S. bowni</i>			M1		[M2,I1,C,P1-4]	M3
<i>P. capensis</i> (Fourie)		[I,P]	M1		M2	M3
<i>P. capensis</i> (Roche)		I	M1	P	M2	M3

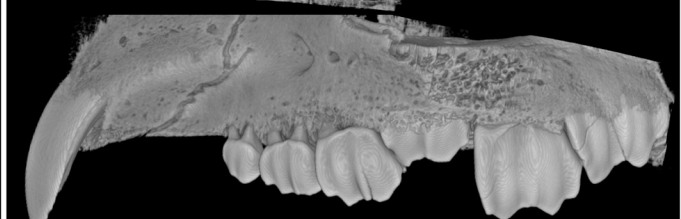
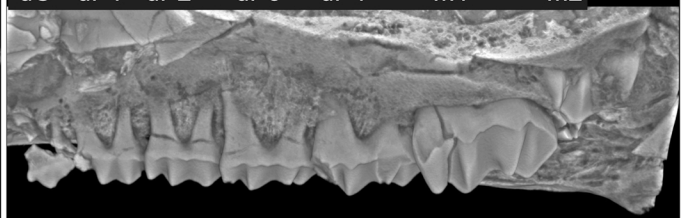
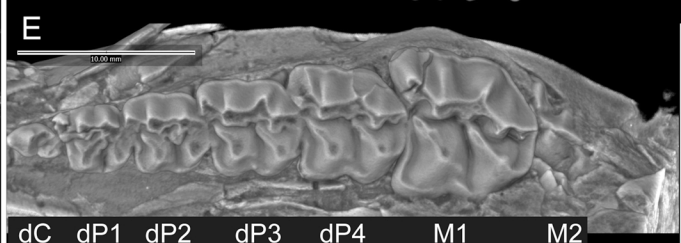
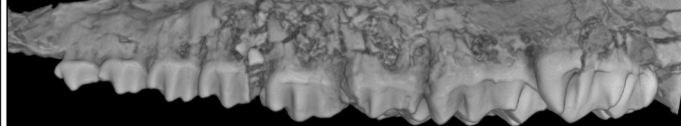
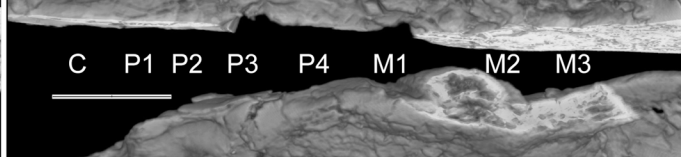
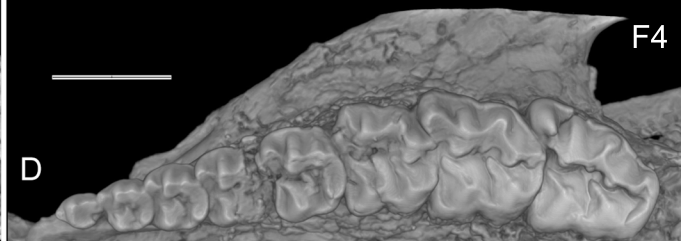
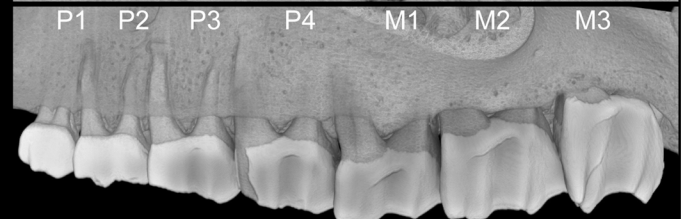
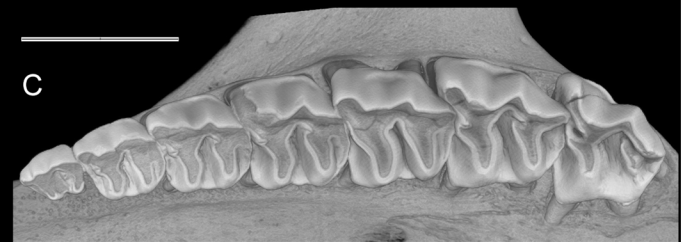
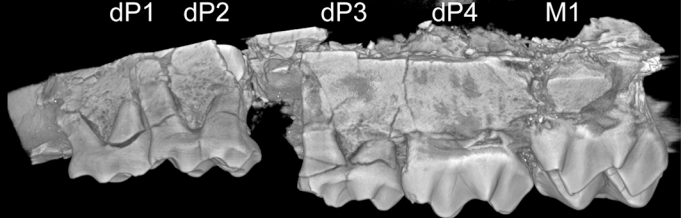
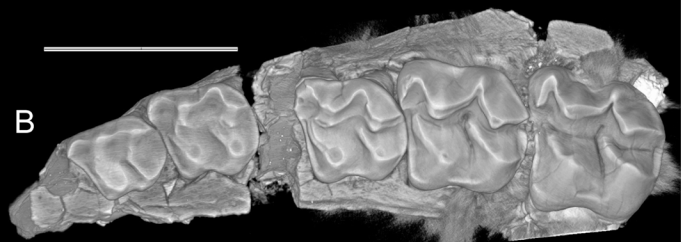
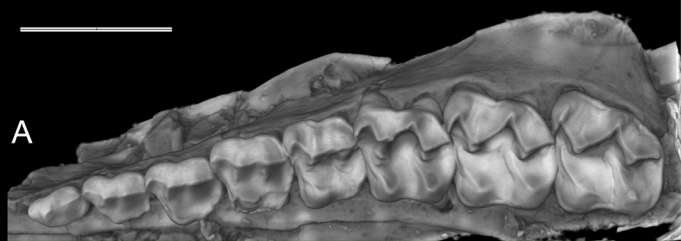
TABLE 4. Correlations of sum of teeth erupting prior to m1 and m2 with gestation length and age at female maturity.

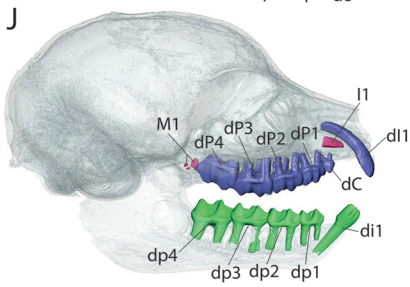
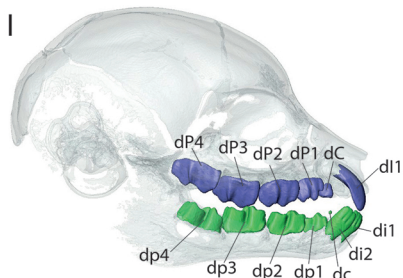
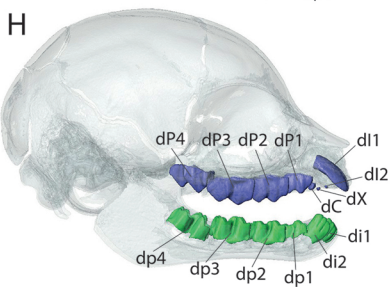
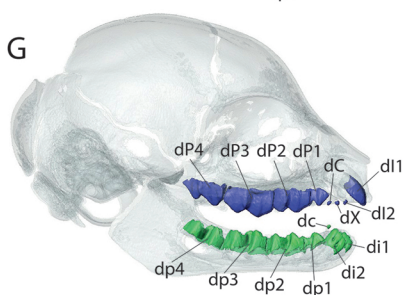
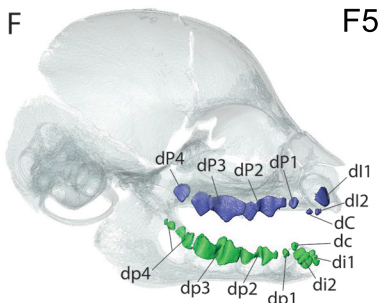
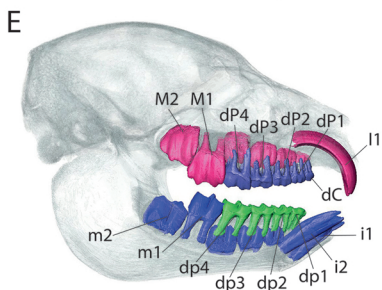
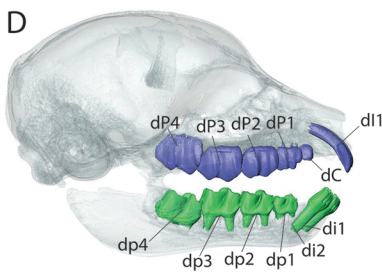
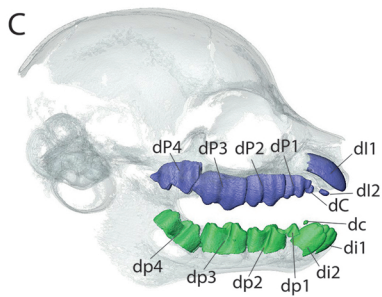
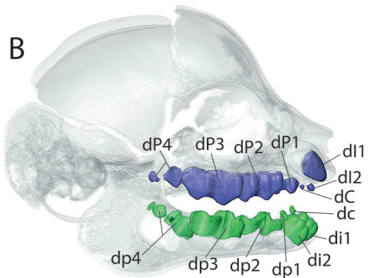
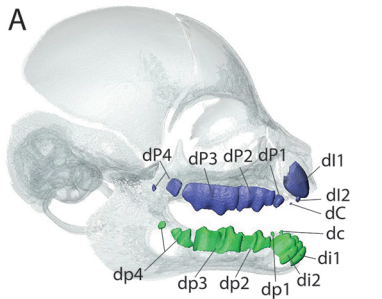
taxa	life history	Pearson's	multiple NN	N		significance
		R	R ²	genera	clades	
afrotherians assuming sengi p1	gestation	0.48	0.23	6	3	n.s.
					3	n.s.
afrotherians without <i>Procavia</i> assuming sengi p1	gestation	-0.17	0.03	5	2	n.s.
					2	n.s.
afrotherians assuming sengi dp1	gestation	0.67	0.45	6	3	n.s.
					3	n.s.
afrotherians without <i>Procavia</i> assuming sengi dp1	gestation	-0.39	0.15	5	2	n.s.
					2	n.s.
afrotherians assuming sengi p1	maturity	0.11	0.01	5	3	n.s.
					3	n.s.
afrotherians without <i>Procavia</i> assuming sengi p1	maturity	-0.99	0.99	4	2	p < 0.01
					2	p < 0.01
afrotherians assuming sengi dp1	maturity	0.4	0.16	5	2	n.s.
					2	n.s.
afrotherians without <i>Procavia</i> assuming sengi dp1	maturity	-0.9949	0.99	4	2	p < 0.01
					2	n.s.
TABLE 4. (Continued)						
Primates & <i>Tupaia</i>	gestation	0.7	0.5	18	13	p < 0.01
					13	p < 0.01
Primates (except <i>Homo</i>) & <i>Tupaia</i>	gestation	0.49	0.24	18	13	p < 0.05
					13	n.s.
Primates & <i>Tupaia</i>	maturity	0.69	0.47	18	13	p < 0.01
					13	p < 0.01
Primates (except <i>Homo</i>) & <i>Tupaia</i>	maturity	0.34	0.11	18	13	n.s.
					13	n.s.





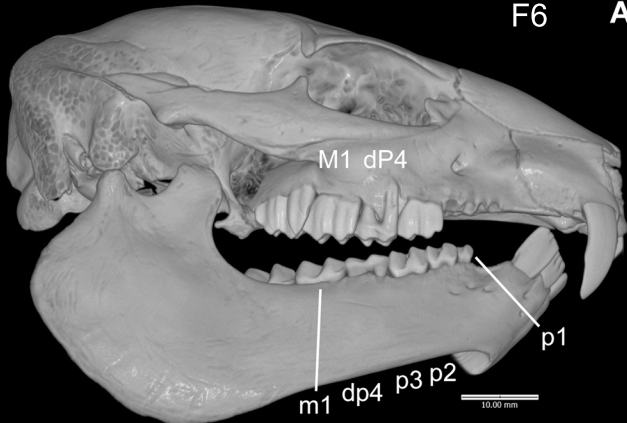




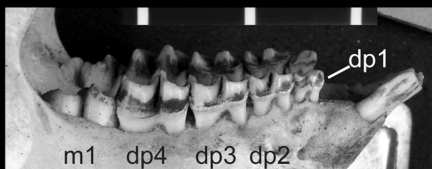


F6

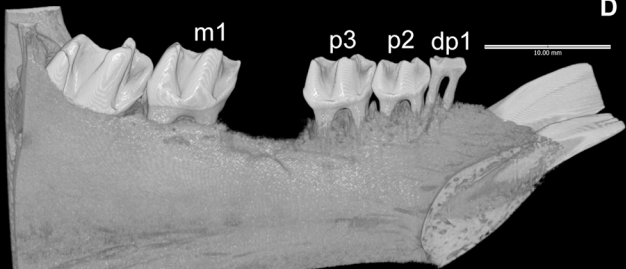
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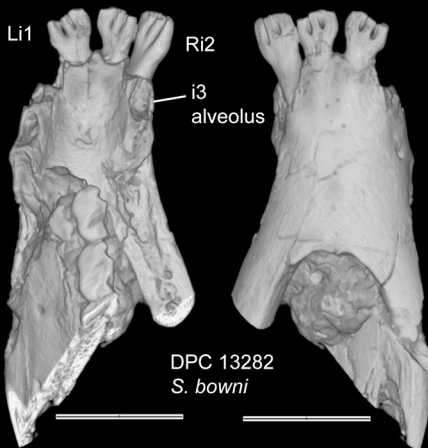
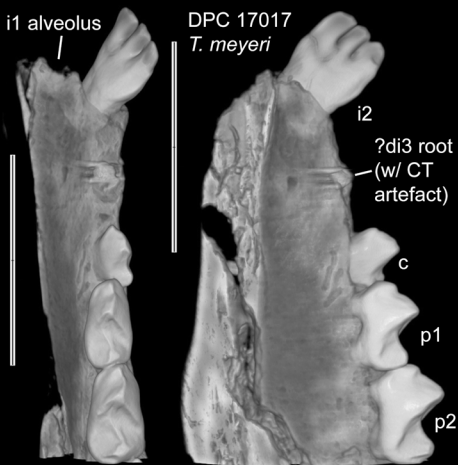
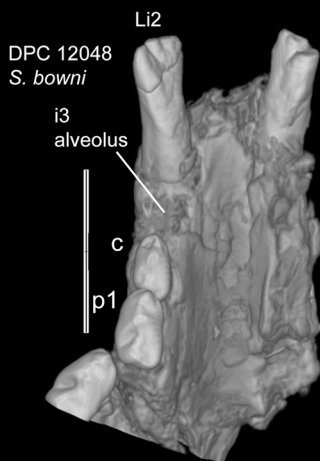
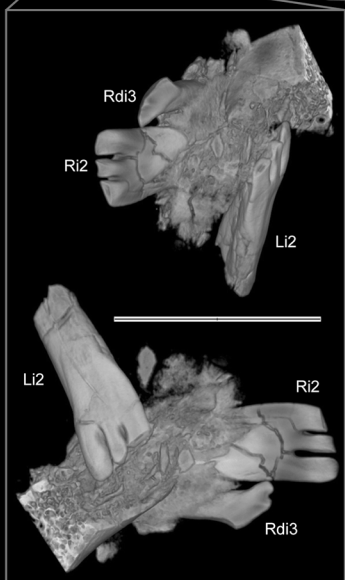
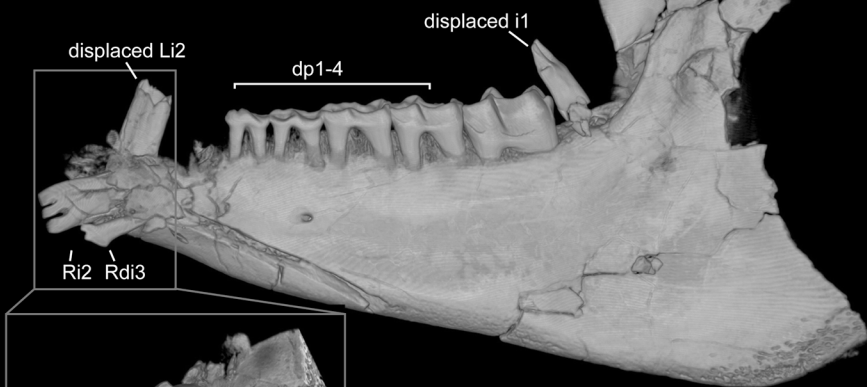


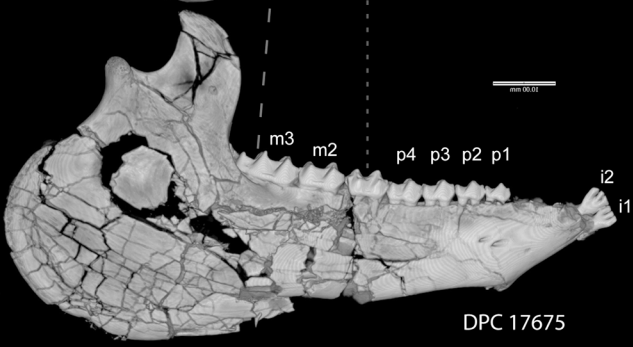
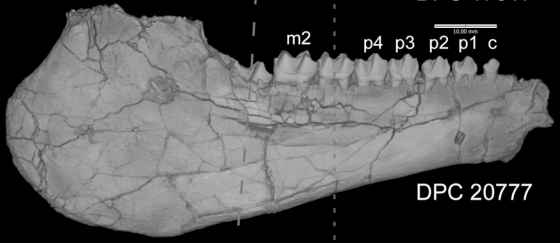
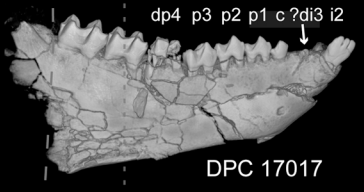
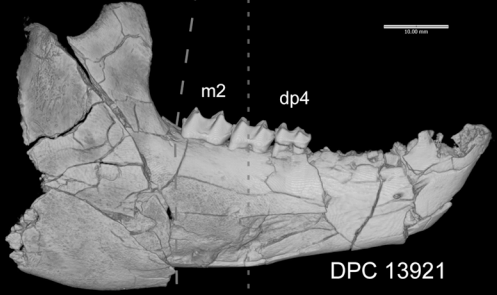
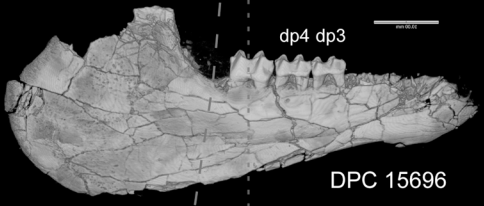
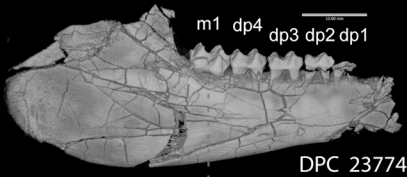
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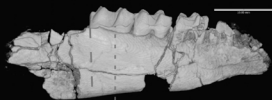
D



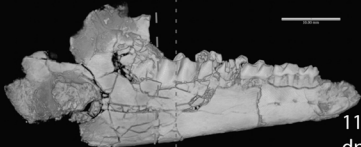




F9



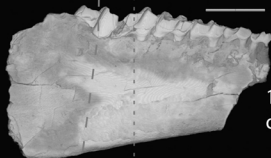
20173
dp2-4,m1



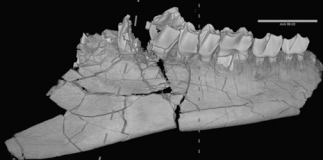
11451
dp1-4,m1



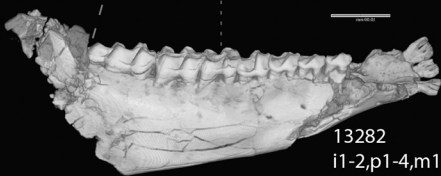
17844
i2,di3,dp1-4,m1



16527
dp1-4,m1-2



20509
p2-3,dp4,m1-2



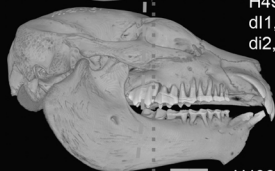
13282
i1-2,p1-4,m1-3



H4981D
dl1,dP1-4,M1
di1-2,dp1-4,m1



H4981C
dP1-4,dC,M1
di1-2,dp1-4,m1



H4981E
dl1,dC,dP1-4,M1
di2,dp1-4,m1



H4980J
l1,P3,dP4,M1-2
i1-2,p1-3,dp4,m1-2



H5051A
l1,P1-3,dP4,M1-2
i1-2,p1-3,dp4,m1-2



H5101A
l1,P1-4,M1-3
i1-2,p2-4,m1-3



H5081B
l1,P1-4,M1-3
i1-2,p1-4,m1-3

