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Unexpected evolutionary patterns of dental ontogenetic traits in cetartiodactyl mammals

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Abstract

Studying ontogeny in both extant and extinct species can unravel the mechanisms underlying mammal diversification and specialization. Among mammalian clades, Cetartiodactyla encompass species with a wide range of adaptations, and ontogenetic evidence could clarify longstanding debates on the origins of modern specialized families. Here, we study the evolution of dental eruption patterns in early diverging cetartiodactyls to assess the ecological and biological significances of this character and shed new light on phylogenetic issues. After investigation of ontogenetic dental series of 63 extinct genera, our parsimony reconstructions of eruption state evolution suggest that eruption of molars before permanent premolars represent a plesiomorphic condition within Cetartiodactyla. This result substantially differs from a previous study based on modern species only. As a result, the presence of this pattern in most ruminants might represent an ancestral condition contributing to their specialized herbivory, rather than an original adaptation. In contrast, late eruption of molars in hippopotamoids is more likely related to biological aspects, such as increases in body mass and slower pace of life. Our study mainly shows that eruption sequences reliably characterize higher level cetartiodactyl taxa and could represent a new source of phylogenetic characters, especially to disentangle the origin of hippopotamoids and cetaceans.

Keywords: Dental eruption, phylogeny, life history, herbivory, Cetartiodactyla

1. Introduction

Studying the evolutionary mechanisms that influenced mammalian diversification and specialization is one of the goals of evolutionary biology, and the study of ontogeny in extinct and extant taxa contributed importantly to this goal in the past decades [1-6]. Dental ontogenetic parameters, such as the relative timing of dental eruption provide clues to the evolution and biology of mammals in their phylogenetic context [7-11]. Dental eruption sequences in mammals can also be used to infer life history and ecological traits, as well as sexual or social characteristics [11-17]. These data present a strong phylogenetic signal in some mammals [12, 16, 18, 19, 20], and they can clarify phylogenetic issues that are the subject of longstanding discussions for both palaeontologists and molecular biologists.

Cetartiodactyla constitute a clade of mammals that comprises extant ruminants, camelids, suoids, hippopotamids and cetaceans. The origins and phylogenetic relationships among these have been widely studied, but there is no consensus [21-26]. Since their origin 55 Ma ago, cetartiodactyls have acquired a wide range of ecological specializations, from cursorial to aquatic adaptations, and from ruminating herbivorous to carnivorous diets. Modern cetartiodactyls show a wide range of body sizes including the largest known mammal, the blue whale, contrasting with their early terrestrial representatives that were mostly small and medium-sized [27]. In terms of dental ontogeny, a study of dental eruption patterns in extant taxa showed that modern members of early diverging clades of cetartiodactyls (i.e. camelids and suids), and also hippos, have a relatively late eruption of molars compared to ruminants [18]. These results suggest that the pattern observed in these early diverging taxa is the ancestral state in cetartiodactyls. Besides, it has been proposed that the pattern of eruption of molars before permanent premolars observed in most ruminants is a derived condition, which is associated with a modified and derived masticatory apparatus that allows them to cope with intense chewing strains and forces related to their specialized herbivory [18].

However, there is little evidence that a correlation exists between life history, body mass and dental eruption pattern in extant ruminants and in other specialized ungulates as well, including perissodactyls (horses, rhinos, and tapirs; [12, 16, 18]). This might be explained by phylogenetic inheritance, meaning that features (i.e. inherited traits) observed in crown taxa were selected before the appearance of these groups, and represent plesiomorphic traits. Therefore, studying dental eruption sequences in relation to skull growth and body mass in extinct cetartiodactyl taxa could contribute to understand the diversity of patterns observed in extant families, and to shed new light on their evolution and their ecological specializations.

Here, we investigate the dental eruption pattern of a wide range of extinct cetartiodactyl families, including the archaeocetes, representing the early diverging cetaceans, which had dental replacement, unlike modern cetaceans. We compare eruption sequences to another ontogenetic parameter, the skull growth, to assess the relative timing of ontogenetic events. Because most modern superfamilies appeared during the Paleogene, our focus is mostly on taxa from this time period that characterize the appearance and early evolution of dental ontogenetic traits in cetartiodactyls. We also document extant families, such as the understudied hippopotamids and camelids. We put these original data in their phylogenetic context using recent studies on both extant and extinct species. This will allow us to reconstruct the character states of early diverging cetartiodactyl lineages, and to evaluate the influence of body mass on dental eruption in these lineages, such as hippopotamoids (extinct “Anthracotheriidae” + Hippopotamidae) known for their important size increase during their evolutionary history. This study permits to discuss phylogenetic affinities of specialized herbivores (e.g. ruminants, camelids) and semi-aquatic (hippopotamoids) to aquatic species (cetaceans), and to assess the evolutionary importance of dental ontogeny in extinct mammal species.

2. Material and methods

(a) Dentition analyses. Ontogenetic dental series of 63 extinct and 14 extant genera of Cetartiodactyla were investigated (table S1). One Perissodactyla (“*Hyracotherium*”), an order that appears as the sister taxon of cetartiodactyls in many studies [e.g. 23, 25], and three early eutherian mammals were also added as outgroups (two Phenacodontidae: *Phenacodus*, *Meniscotherium*; and one Leptictidae: *Leptictis*). Data on dental eruption sequences were obtained from material housed in different institutions (MNHN: Muséum National d’Histoire Naturelle, Paris; MNHT: Muséum d’Histoire Naturelle, Toulouse; University of Montpellier; University of Lyon; Confluences Museum, Lyon; University of Poitiers; MHNO, Muséum d’Histoire Naturelle, Orléans; Museum Crozatier of Le Puy-en-Velay, France; Peabody Museum, Harvard; AMNH: American Museum of Natural History, New York, USA; CNRD: Centre National de Recherche pour le Développement, N’ djamena, Chad; National Museum of Ethiopia/Authority for Research and Conservation of the Cultural Heritage, Addis Ababa, Ethiopia; NMK: National Museums of Kenya, Nairobi; Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; Museum für Naturkunde, Berlin, SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany; RMCA: Royal Museum of Central Africa, Tervuren, Belgium; NHM: Natural History Museum, London, United Kingdom; Museum of Natural History, Bern; Museum of Natural History of the town of Geneva, Switzerland; Ranga Rao collection, Dehra Dun, India) and from previously published studies (table S1). Our data are based on upper and lower cheek teeth (i.e. premolars and molars), as Monson and Hlusko [18] did (but only for the lower dentition), because they display high levels of morphological and developmental integration in mammals [28-29]. P^x and M^x refer to the xth upper premolars and molars, P_x and M_x to the xth lower premolars and molars, and Px and Mx to both the xth upper and lower premolars and molars. Ontogenetic data on the canine were also considered when available as this tooth is more or less independent from the premolar-molar module, and is important in terms of ecology or social interactions, including mating competition [30]. The

most anterior part of the jaw, which carries the incisors, was not considered here because it is frequently damaged or missing in fossils. In most cases, data were gathered from ontogenetic stages that showed fully erupted teeth. This avoids misinterpretation related to relative eruption of premolars and molars [9, 17].

(b) Virtual reconstructions of the dentitions and imaging. Specimens of *Diplobune minor*, *Microbunodon minimum*, and *Indohyus indirae* were scanned using X-ray microtomography (EasyTom 150kV, RX solutions) at 120-130kV, and at voxel sizes of 23.8 and 45.6 μm (mandible and maxilla), 27.8 and 47 μm (mandible and skull), and 45.6 μm (maxilla) respectively. 3D virtual reconstructions of the dentition were made on Avizo version 9.5 (<https://www.fei.com/software/amira-avizo/>), and then imaged in order to display different states or patterns of dental eruption regarding relative eruption of permanent premolars and molars, and the direction of eruption for permanent premolars (figure 1).

(c) Parsimony reconstruction for character state evolution. The character state reconstruction of early diverging cetartiodactyl lineages was performed using Mesquite version 3.04 [31], with Deltran optimization [32] for branches with ambiguous state. The first analysis traced the evolution of the dental eruption sequence on a simplified phylogenetic tree derived from concatenation of both molecular and morphological data on some extinct and extant cetartiodactyls, including stratigraphic ranges (modified from [25]; figure 2). This analysis, which includes non-cetartiodactyl outgroups (one perissodactyl, two phenacodontids, and one leptictid), and both extinct and extant cetartiodactyls, is relevant for comparison with the analysis based on extant taxa only [18]. The second analysis explores the relationships between the evolution of dental eruption sequence and estimated body mass ranges. It is realized on a simplified phylogenetic tree of extinct cetartiodactyls based on morphological data only, with

a focus on Hippopotamoidea (modified from [26]; figure 3). This second analysis is more relevant for assessing the relationships between dental eruption states and body masses, because the phylogeny used includes many more extinct cetartiodactyl families than in the first analysis, and encompasses a higher number of cetartiodactyls in a constrained geological period (mostly Paleogene). The body mass estimations were mostly based on the formula from Martinez and Sudre [33] using astragalus dimensions (i.e., length and proximal width; or on M₁ length when the astragalus is missing; table S2).

(d) Ontogenetic measurements. The stages of dental eruption were reported together with mandibular growth which was used as a proxy for skull growth. In order to maximize the sample size, mandibular depth was measured instead of condylo-incisive length. This was measured at the distal side of M₁, for two different eruption stages (see figure 4). The first of these is after M₁ eruption, since that stage is significantly correlated to some life history traits in cetartiodactyls, such as age at sexual maturity [16]. The second is after eruption of the entire dentition as this generally corresponds to the adulthood (figure 4; table S3).

3. Results

The most striking result is that the wide majority of Paleogene families of cetartiodactyls (Amphimerycidae, Anoplotheriidae, Cainotheriidae, Cebochoeridae, Choeropotamidae, Diacodexidae, Dichobunidae, Lophiomerycidae, Merycoidodontidae, Mixtotheriidae, Raoellidae, Xiphodontidae) has a pattern with the M₃ erupting before most permanent premolars, like most extant ruminants (figures 2 and 3). This also includes early cetaceans (*Dorudon*, *Zygorhiza*) and early camelids (*Poebrotherium*), one of the closest sister taxa of cetartiodactyls, the perissodactyl “*Hyracotherium*”, and early diverging eutherian mammals, the Phenacodontidae and Leptictidae. Conversely, the anthracotheres, most suoids,

Choeropotamus and *Gobiohyus* show an M3 erupting last, like *Ovis* (an extant caprine ruminant). Extant Camelidae, as well as Hippopotamidae, generally display an intermediate, but variable eruption pattern in which M3 erupts at the same time or after P4, while only strict intermediate eruption (i.e. M3 erupting at the same time as P4) is observed for *Archaeotherium*, even if data are scarce.

The parsimonious reconstruction of character state evolution performed on the first phylogeny shows that the plesiomorphic cetartiodactyl state corresponds to M3 erupting before the permanent premolars (figure 2). Additionally, despite the absence of a non-cetartiodactyl outgroup, the ancestral state reconstruction analysis using the second phylogeny also recovers the same result for the basal most cetartiodactyl node (figure 3). In contrast, M3 erupts later than all or most of the premolars in medium to large-sized Paleogene cetartiodactyls such as Hippopotamoidea, and many Suoidea (figure 3). Nonetheless, many medium-sized Paleogene taxa do not present this pattern (e.g. Anoplotheriidae, Lophiomerycidae, Merycoidodontidae, Mixtotheriidae), as well as large-sized archeocetes, and medium to large-sized Neogene to extant cetartiodactyls (e.g. many ruminants).

The precise relative eruption sequences of the molars and of the premolars also show variation. In general, M1 erupts immediately after the deciduous premolars, but the eruption of M2 is more variable, either erupting before or after some of the permanent premolars. This pattern is obvious in Hippopotamidae (table S1). If we except P1, the replacement of which is difficult to identify for most taxa, M2 erupts before P2 in most studied cetartiodactyls, while in extant hippopotamids, it erupts at the same time (*Choeropsis*) or after P2 (*Hippopotamus*). Permanent premolars erupt (or mineralize) sequentially in the mesio-distal direction (from P1 to P4) in most extinct and extant cetartiodactyls. However, the opposite pattern (from P4 to P1) is observed in a few Paleogene taxa, such as *Indohyus* (Raoellidae), *Archaeotherium*, *Entelodon* (Entelodontidae), *Dorudon* and *Zygorhiza* (Cetacea; figures 2 and 3, table S1). It is also

observed in a few extant cetartiodactyls (e.g. suoids).

The eruption of the permanent canine is also highly variable. This tooth erupts at the same time or after M2 or P2 in early mammals (Phenacodontidae) and early cetartiodactyls (e.g. *Dichobune*, *Merycoiodon*). Alternatively, it erupts simultaneously or after M1 in extinct and extant hippopotamids (e.g. *Archaeopotamus*, *Hexaprotodon*) and suoids (e.g. *Palaeochoerus*). In derived anthracotheres (e.g. *Libycosaurus*), the canine erupts after M3, as it does in extinct cetaceans, and *Diplobune*. It is also the case in extant camelids and some high-crowned ruminants (e.g. Tragulidae, Moschidae) and early cetartiodactyls (e.g. *Mixtotherium*).

Measurements on ontogenetic series show that anthracotheres, suids, early diverging hippopotamids and the extant ruminant *Capra* show the lowest value for the ratio of the depth of the mandible at M₁ between juveniles and adults (figure 4). This also includes some Eocene cetartiodactyls, *Cebochoerus* and *Diplobune*, for which samples are small (less than five specimens measured). Values for hippopotamids, including extant species, as well as anthracotheres, show high variation. Camelids display the highest values, slightly higher than extant hippos, extinct and extant ruminants, and other Eocene cetartiodactyls (e.g. *Dacrytherium*, *Dorudon*).

4. Discussion

(a) Early eruption of molars is the plesiomorphic state in cetartiodactyls and in eutherians

Eruption of M3 before permanent premolars occurs in most ruminants, representing the vast majority of extant cetartiodactyls [12, 16, 18]. Monson and Hlusko [18] (figure 2b) proposed that a late eruption of the molars is the ancestral state in cetartiodactyls based on its presence in early diverging crown families (camelids, suids, tayassuids) and hippos. However, our analyses of dental eruption sequences of extant camelids and hippos rather show that intermediate to late eruption of molars occurs in these taxa, as it does in most suoids (table S1).

More surprisingly, the parsimonious reconstruction shows that M3 erupting before the permanent premolars is the ancestral state reconstructed for cetartiodactyls (figures 2). The fact that most Paleogene genera present this pattern contradicts the conclusions of Monson and Hlusko [18], who also considered the origin of this state going back to 55-40 Ma, around their hippopotamid-ruminant divergence.

Veitschegger and Sánchez-Villagra [16] proposed that Cainotheriidae, an extinct group of small European cetartiodactyls, retain ancestral mammalian eruption sequences (i.e. early eruption of M3), consistent with our finding on a large sample of Paleogene cetartiodactyls (figure 2a). The early molar eruption also occurs in some early diverging eutherian mammals (phenacodontids, leptictids, and also arctocyonids; figure 2a, table S1) and concurs with the hypothesis that this pattern is a plesiomorphic mammalian character [34]. That hypothesis is further supported by data on other mammals such as early diverging primates (i.e. non anthropoids; [13, 19, 20]) and rodents [35]. The early eruption of molars is likely plesiomorphic in ruminants, and previous functional interpretations [18] should be revised. As a result, the early eruption of molars in ruminants might not have represented an adaptation related to modification of the masticatory apparatus.

(b) Dental eruption sequences in cetartiodactyls as a potential source of phylogenetic characters

Dental eruption sequences can offer insights into mammalian higher phylogeny, especially considering the position of Hippopotamoidea (both “Anthracotheriidae” and Hippopotamidae), Suoidea and Cetacea. Several authors have proposed that “Anthracotheriidae” are closely related to taxa originally assigned to Asian “Heloyidae”, such as *Gobiohyus* [36-38] or to European Choeropotamidae [26, 39, 40] (figure 3). Late eruption of M3 (after the permanent premolars) occurs in anthracotheres, *Gobiohyus* and *Choeropotamus*.

Although some morphological features do not suggest that anthracotheres are directly derived from these families [39, 41], our evidence is consistent with close phylogenetic ties between these taxa, as it was suggested for anthracotheres and *Choeropotamus* by recent studies [26, 40, 42].

Interestingly, the suoids studied here (including *Palaeochoerus*), show that the canine erupts early, which is also observed in hippopotamids. This character could support close affinities of Suoidea with Hippopotamidae as suggested by a few studies (e.g. [43, 44]). Our study shows that the M3 tends to erupt late in both taxa, although there are variations with eruption of M3 and P4 being more closely spaced in time in hippopotamids, and with greater differences in time lags between them in suoids, like anthracotheres. These variations may suggest that convergence yielded the similarity in patterns. Such a convergence is suggested by similar ratios in relative timing of eruption of M₁ (compared to mandibular growth; figure 4) found in some geologically old suoid, *Palaeochoerus* (i.e. Oligocene), and in young hippos (*Hexaprotodon* and *Hippopotamus*), but excludes other hippopotamids. Interestingly, the ratios for other extinct to extant hippopotamids (i.e. *Archeopotamus*, aff. *Hippopotamus*, *Choeropsis*) are closer to some anthracotheres (figure 4), including *Bothriogenys* and *Brachyodus*, which are frequently considered as an offshoot of hippopotamids (e.g. [26, 42]). While these values from dental ontogenetic series might support phylogenetic ties between some anthracotheres and early diverging hippos [26, 42], all the evidence needs to be considered to investigate this further.

A unique dental eruption pattern emerges in early cetartiodactyls: the disto-mesial eruption of permanent premolars, only observed in Entelodontidae, Raoellidae, and Archaeoceti during the Paleogene. This pattern is not rare in mammals, because it occurs for instance in some geologically younger cetartiodactyls (see suoids in figure 2), as well as in some lipotyphlans, macroscelidids, chrysochlorids, carnivores or most non-anthropoids and

platyrrhine primates [12, 45]. This pattern has been recognized as a secondarily derived condition in eutherians [46]. Nonetheless, it could characterize a clade including Entelodontidae, Raoellidae, and Cetacea, partly consistent with findings of previous studies [21, 23, 25, 26, 47] (figures 2 and 3). This disto-mesial eruption pattern of premolars might give more supports for an origin of cetaceans close to raoellids [47, 48]. These different examples of character evolution show the interest of considering dental eruption for further phylogenetic investigations, as previously suggested [16, 18, 19].

(c) Intricate biological and ecological significance of dental eruption patterns

Changes towards eruption of M3 after the premolars evolved in different extant and extinct cetartiodactyls taxa (e.g. anthracotheres, Choeropotamidae, *Gobiohyus*, Hippopotamidae, Suoidea, Camelidae, Caprinae). Interestingly, the appearance of this derived eruption state is generally associated with increases in body mass, especially in Hippopotamoidea (figure 3). Such association between late eruption of molars and large size also occurs in other mammals, such as rhinos, elephants, the extinct pantodont *Coryphodon* (table S1), but also in primates [12, 19, 49, 50]. It suggests that most extinct hippopotamoids underwent a relatively slow pace of growth, like extant relatives and analogues (e.g. rhinos, elephants; [12, 51]). However, anthracotheres (except *Brachyodus*) have a more rapid eruption of M₁ relative to skull growth than most hippopotamids (figure 4). In this regard, the dental eruption sequence of many anthracotheres is similar to extant suoids. This supports the view that life history traits of anthracotheres and close-sized suoids are similar (e.g. *Bothriogenys* and *Sus*, [15]). The same may be true for early known hippopotamids.

In most ruminants, M3 erupts before permanent premolars, but M₁ erupts late with respect to skull growth (figure 4), unlike extinct South American ungulates that display the same eruption pattern [11]. This relative eruption timing might be due to the rapid and

precocious development of the skull of cetartiodactyls, especially jaw bones, compared to other mammals [52]. The development of the jaw is accelerated in ruminants compared to other modern cetartiodactyls, and it might allow a more rapid eruption and setting of the entire dentition. More generally, the plesiomorphic pattern of early eruption of molars compared to permanent premolars in ruminants might be originally influenced by the faster skeletal growth of early mammals [34, 45, 53]. This limits the number of teeth within the jaw, but allows an earlier eruption of the molars before the permanent premolars. This rapid setting of the entire dentition in ruminants might serve their herbivorous specialization and might represent a condition that likely contributes to enhanced food processing in precocial young individuals and not an adaptation from their ancestors. This functional explanation has also been proposed for late diverging South American ungulates (i.e. notoungulates), which convergently acquired eruption of molars before premolars, and this has also been suggested to be related to environmental changes [11]. However, this pattern does not occur in caprine ruminants where the last molar erupts well after the other teeth, and M_1 erupts later compared to skull growth. This has been assumed to be related to erratic resource availability at high elevation habitats, rather than to life history traits [18].

In archeocetes, which show the same ontogenetic patterns as most ruminants, dental eruption is also sped up in derived Basilosauridae (i.e. *Chrysocetus*). This may be a transitional state toward the loss of dental replacement and polydonty in post-Eocene cetaceans [54]. Variation in dental ontogenetic sequences in suoids and camelids makes it difficult to assess evolutionary sequences. Nonetheless, the strong ecological specialization in camelids and some suoids, as in ruminants, suggests that the eruption pattern might be related to functional aspects of food processing rather than to life history traits. The inconsistencies between the timing of M_1 eruption and of the entire dentition compared to life history traits might be explained by the fact that cetartiodactyls have a precocial skull development combined to prolonged growth

compared to most mammals [52, 55]. More absolute data with precise skull growth and eruption timing are needed to determine the relation between age at sexual maturity and M₁ eruption, and the relation between the eruption of the entire dentition and the putative prolonged body growth of extant cetartiodactyls.

(d) Inter- and intraspecific variation and evolutionary interest of dental eruption patterns

Inferences on life history from dental ontogeny or body sizes are not straightforward in mammals, especially because of the high level of inter- and intraspecific variation [13, 16, 18]. Changes in size and life history have occurred in parallel during evolution, with various skeletal or ontogenetic modifications [56]. However, some taxa are exceptions to these observations, and ecological factors may play a role [51, 57]. While molars erupt early in most ruminants, the sequence of premolar replacement can vary in closely related species (figure 2), but also within a species [16]. As a result the exact sequence of dental eruption is not a good predictor of life history traits, as shown in primates [13, 19]. Based on a large sample of *Ovis*, Monson and Hlusko [18] proposed that determination of dental eruption sequence based on at least two observations is fairly accurate, which is obvious in most cases, but variations do occur, especially between upper and lower dentitions, as exemplified in hippopotamids in our study.

Past studies have shown that hippopotamids frequently show that the last lower molars erupt after the last premolars [12, 18, 58]. However, the opposite pattern, or intermediate patterns, occur more frequently in upper cheek teeth, which has never been reported (table S1). Interspecifically, the M2 erupts after P2-P3 in *Hippopotamus*, unlike extinct hippopotamids and the pygmy hippo (table S1). This could be related to a higher tooth crown for *Hippopotamus* compared to other genera [59]. Indeed, convergent trends related to M2 eruption have been reported in high-crowned mammals, such as extinct rhinocerotids and extant hyraxes [17, 50]. It has been proposed that this pattern is related to grazing which would cause severe wear on

deciduous teeth. These teeth would then be more rapidly replaced, and the permanent premolars would erupt before most molars. This may be the case for *Hippopotamus* too.

Similarly, canines erupt early in ontogeny in hippopotamids and suoids, and late in the anthracothere *Libycosaurus* and in archaeocetes. Hippos and suoids use their evergrowing canines for fighting and/or food gathering early in life, while in *Libycosaurus* the canines are deeply rooted in males and they are assumed to be involved in sexual displays, and probably less in fights [60]. These constraints on canine function tend to be relaxed in the evolution of cetaceans and ruminants, as suggested by the small size or even absence of these teeth in most extant species. It is possible that specialized ways to process food affected the evolution of canines. However, this is not the case of camelid, tragulid and moschid males, which generally exhibit larger functional canines used in sexual displays or fighting.

These examples added to the current knowledge on mammals show that fine-tuning of specific changes in the dental eruption sequence are largely related to ecological factors, social behaviour, structural adjustments, and relaxed or neutral selections; and that life history traits affect them to a lesser degree. Histological studies may provide data on life history traits [61, 62], but in the absence of such data, inferences of pace of life from dental ontogeny should be limited to higher macroevolutionary events (e.g. origin and diversification of high-level taxa). In that context, major modifications in the dental eruption sequence more likely highlight important biological changes, or pinpoint pivotal events during the evolutionary history of some families related to their diversification or specialization.

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Data accessibility. Supporting data are accessible in electronic supplementary material, tables S1, S2 and S3.

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Figure 1 Main variations of dental eruption observed in 3D microtomographic reconstruction of cetartiodactyl jaws. (a) Dental eruption state showing M3 erupting before the premolars (*Diplobune minor*, UM ITD45, UM ITD41) (b) Dental eruption state showing M3 erupting after the other teeth (*Microbunodon minimum*, MNHN.F.AGN306, Ma236-69) (c) Dental eruption state predicting disto-mesial eruption of premolars (*Indohyus indirae*, RR262).

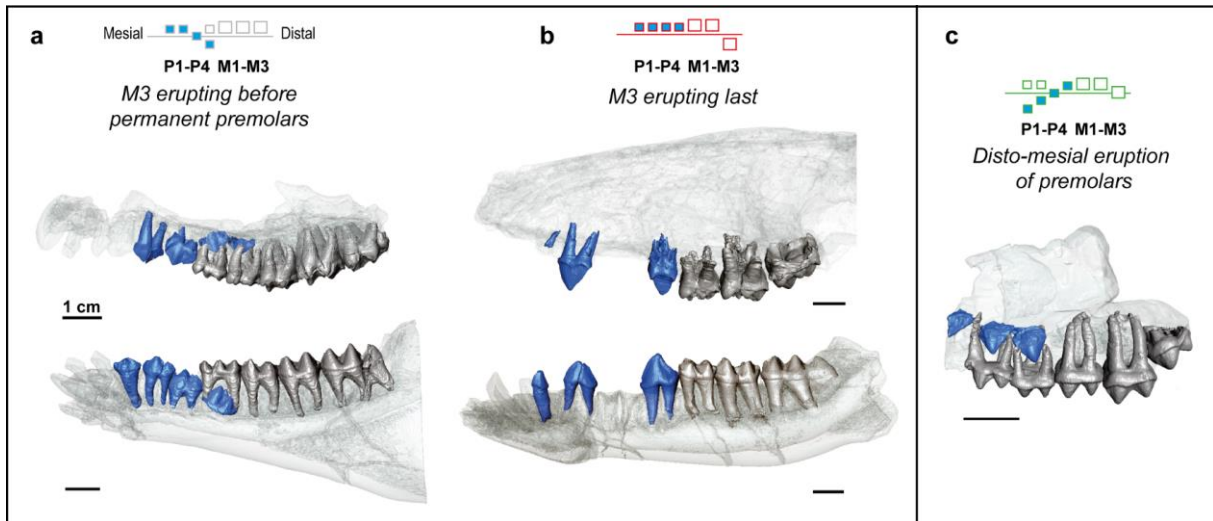


Figure 2 (a) Phylogenetic tree of extant and extinct cetartiodactyls with stratigraphic range (modified from [25]) showing parsimony reconstruction of evolution of the dental eruption sequence. (b) Simplified phylogenetic tree of extant cetartiodactyls showing parsimony reconstruction of evolution of the dental eruption sequence (modified from [18]).

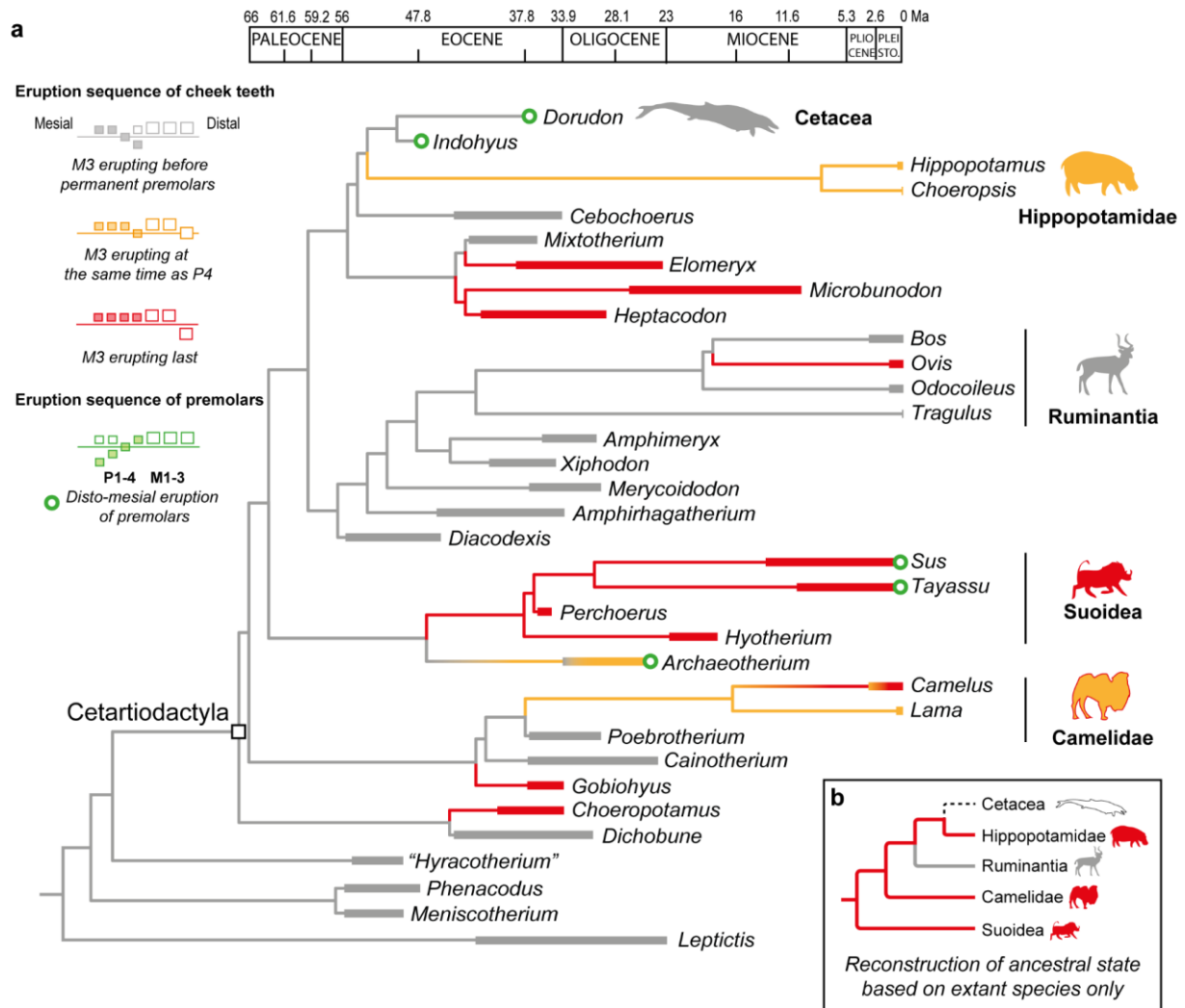


Figure 3 Phylogenetic tree of extinct cetartiodactyls with a focus on Hippopotamoidea (modified from [26]) showing parsimony reconstruction of evolution of the dental eruption sequence compared with estimated body masses. In brackets, number of genera investigated and corresponding state of dental eruption.

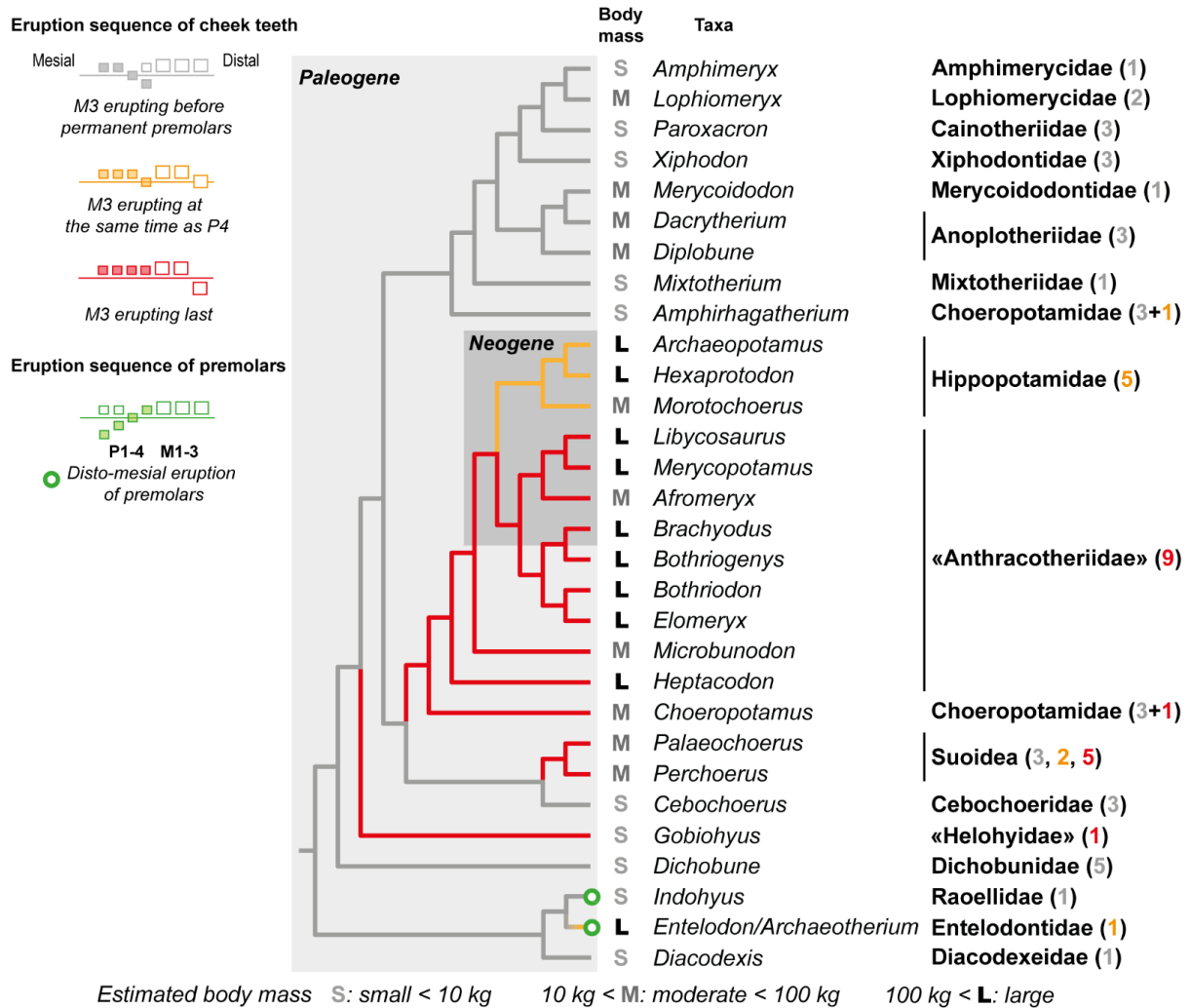


Figure 4 Ontogenetic data corresponding to ratio of juvenile mandibular (Md) size (as measured immediately after M₁ eruption) and mean adult mandibular (Adult Md, measured distally to M₁) size. Extant genera are in bold; open circles correspond to small samples (i.e. less than five specimens). + represents “M3 erupting at the same time as P4” state, and * represents “M3 erupting last” state (hypothesized reconstructed state for *Anthracotherium*). In violet: early diverging cetartiodactyls; in blue: Ruminantia; in grey: Cetacea; in orange: “Anthracotheriidae”; in red: Hippopotamidae; in yellow: Suoidea; and in green: Camelidae.

