

When xenarthrans had enamel: insights on the evolution of their hypsodonty and paleontological support for independent evolution in armadillos

Martín R. Ciancio · Emma C. Vieytes · Alfredo A. Carlini

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Abstract All xenarthrans known to date are characterized by having permanent teeth that are both high crowned and open rooted, i.e., euhyposodont, and with a type of hypsodonty different from that of the rest of Placentalia: dentine hypsodonty. Also, most xenarthrans lack enamel; however, its presence has been reported in the fossil armadillo *Utaetus buccatus* and in living *Dasypus*. Considering the divergence of Xenarthra from other eutherians that possessed enameled teeth, the absence of enamel is a derived character. Diverse specializations are known in the dentition of xenarthrans, but the primitive pattern of their teeth and dentitions is still unknown. Here, we describe the mandible and teeth of a fossil armadillo, *Astegotherium dichotomus* (Astegotheriini, Dasypodidae), from the early Middle Eocene of Argentine Patagonia, with teeth showing both true enamel and closed roots. It is the oldest xenarthran with mandibular remains exhibiting protohypsodonty and is therefore likely

representative of ancestral cingulates and xenarthrans generally. *Astegotherium* supports a recent hypothesis based on molecular data that enamel loss occurred independently not only within xenarthrans but also within dasypodid armadillos.

Keywords Armadillo · Astegotheriini · Radial enamel · Protohypsodont · Homoplasy · Eocene

Abbreviations

MMP Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia” Mar del Plata, Argentina
MPEF Museo Paleontológico Egidio Feruglio Trelew, Argentina

Introduction

Xenarthra (Mammalia) is one of the four major clades of extant placental mammals (Murphy et al. 2001; Springer and Murphy 2007). They are characteristic of the Neotropical fauna and have had a long evolutionary history that spans most of the Cenozoic, from the late Paleocene to the present (Delsuc et al. 2004; Pascual 2006; Billet et al. 2011). This clade originated in South America, an island-continent during most of the Cenozoic in which its members were able to exploit a wide variety of environments (Pascual 2006).

Although the monophyly of the Xenarthra is widely supported (Delsuc and Douzery 2008; Gaudin and McDonald 2008), their phylogenetic position relative to the other major clades of Placentalia is still under discussion. Different proposals have placed them as the basal-most clade of placentals as the sister group of Epitheria (Shoshani and McKenna 1998; O’Leary et al. 2013); as a more derived clade, sister group

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M. R. Ciancio (✉) · A. A. Carlini
División Paleontología de Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina
e-mail: mciancio@fcnym.unlp.edu.ar

M. R. Ciancio · E. C. Vieytes · A. A. Carlini
CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

M. R. Ciancio · E. C. Vieytes · A. A. Carlini
Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina

E. C. Vieytes
Sec. Mastozoología, Zoología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina

of Boreoeutheria (Laurasiatheria+Euarchontoglires) within the clade Exafroplacentalia (Murphy et al. 2001; Springer and Murphy 2007; Romiguier et al. 2013), or as the sister group of Afrotheria in the clade Atlantogenata (Hallström et al. 2007; Asher et al. 2009; Meredith et al. 2013).

The large amount of specializations acquired by xenarthrans has likely hidden or erased not only many placental symplesiomorphies but also some potential apomorphies exclusively shared with some placental subsets (e.g., like delayed dental eruption only visible in *Dasypus*). Their dentition is particularly noteworthy (Gaudin and McDonald 2008; Vizcaíno 2009; Ciancio et al. 2012) and includes (1) reduction/loss of premaxillary teeth, (2) loss of the deciduous dentition (except *Dasypus*), (3) reduction/loss of enamel, (4) euhypsodonty (see below), and (5) teeth that are frequently homodont and simple in shape, except for some sloths and glyptodonts.

The oldest known representatives of Xenarthra are armadillos belonging to Astegotheriini (Dasypodinae, Dasypodidae, Cingulata) (Vizcaíno 1994; Carlini et al. 2010; Ciancio et al. 2013) whose earliest records correspond to the early Paleogene (late Paleocene or early Eocene) of Itaboraí, Brazil (Olivera and Berqvist 1998; Berqvist et al. 2004; Woodburne et al. 2014). Subsequently, they become highly diverse in the Early-Middle Eocene of Patagonia (Carlini et al. 2010; Ciancio et al. 2013), and their last records are from the Middle Miocene of La Venta, Colombia (Carlini et al. 1997). The general consensus is that the Astegotheriini is the earliest diverging Dasypodinae, mainly on the basis of osteoderm morphology; its fossil record is almost exclusively composed of these elements (Vizcaíno 1994; Carlini et al. 1997, 2010). However, this hypothesis has not been tested through phylogenetic analyses because their skeletal remains are scarce and fragmentary.

Here, we describe the morphology and dental histology of the teeth preserved in a partial mandible of the fossil armadillo *Astegotherium dichotomus* Ameghino, 1902 (Astegotheriini, see Vizcaíno 1994). This material comes from Cañadón Vaca (Chubut province, Patagonia Argentina), which has been assigned to a Vacan subage of the Casamayoran South American Land Mammal Age (SALMA) (Cifelli 1985), early Middle Eocene age. This is the oldest known xenarthran with toothed mandibular remains. Here, we discuss the presence of true enamel and other dental characters in this taxon, which has important implications on our understanding the dental morphology of basal xenarthrans.

Materials and methods

The studied remains (MMP 676-M) correspond to a partial mandibular ramus (probably left) with three molariform teeth and three osteoderms assigned to *A. dichotomus* Ameghino,

1902, (Fig. 1a). These were previously described by Vizcaíno (1994), although the presence of enamel was not detected, and the intra-alveolar portion of the molariforms was not described. The materials were collected by G. Scaglia in 1958 and come from the fossil-bearing levels of Cañadón Vaca, a tributary to the left (northwest) bank of the Río Chico, Chubut, Argentina (Fig. 2). This is the type of locality of the Vacan subage of the Casamayoran SALMA (see Cifelli 1985, Fig. 3), and it has been assigned to an early Middle Eocene age, based on $^{40}\text{Ar}/^{39}\text{Ar}$ isotopic dates that yield an approximate age of 45 Ma for ash-bearing sediments (unpublished data, Gelfo et al. 2009), and a lapse of ca. 43–46 Ma was proposed based on stratigraphic data (Woodburne et al. 2014; Bellosi and Krause 2014).

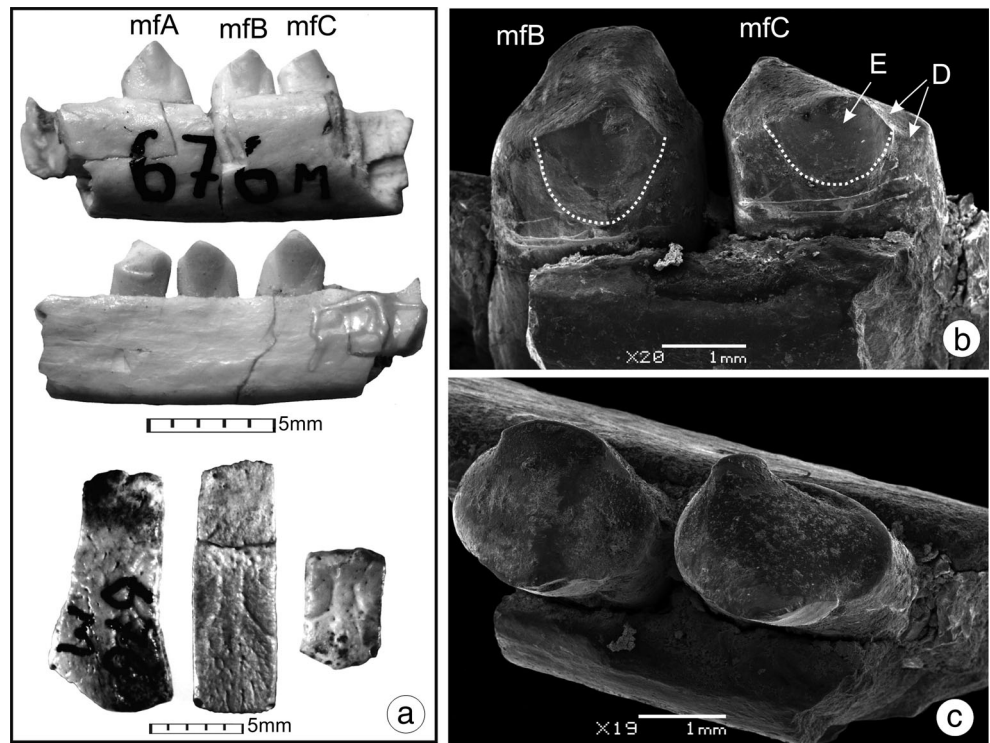
The teeth were described using a Nikon SMZ645 binocular stereo microscope. For the study of enamel microstructure, a tooth (mfA) was embedded in epoxy resin. Then, the specimen was ground along longitudinal (vertical) and transversal sections with sandpaper and grinding powder and etched for 5–6 s with 2 N HCl to create a morphological relief. After rinsing and drying, specimens were sputter-coated and examined under a scanning electron microscope (SEM) Jeol JSM-T100. The nomenclature of enamel microstructure follows Koenigswald and Sanders (1997). In order to interpret the three-dimensional enamel pattern, the specimens were analyzed in both transverse and longitudinal sections.

For the examination of root morphology, we use dental radiographs of *A. dichotomus* (MMP 676-M) and *Utaetus buccatus* (MPEF PV 5426, Carlini et al. 2010).

Terminology Hypsodonty refers to those teeth that are high crowned and was coined in opposition of the term brachydonty (low-crowned teeth), the primitive mammalian condition (Janis 1988; Damuth and Janis 2011). Formally, the term hypsodont describes a tooth that eventually develops one or more roots but that has a crown higher than those roots or than its horizontal dimensions, according the original definition of Simpson (1970).

There are different degrees of hypsodonty, for which several other terms apply (mesodont, prohypsodont, and protohypsodont). Most of these terms were used with varying definitions or are applicable only for specific groups. A special case of hypsodonty is open-rooted or continuously growing teeth which are often described as hypselodont, but this term has been used inconsistently, sometimes synonymously with hypsodont (Mones 1982; Janis and Fortelius 1988). Mones (1982) proposed the terms protohypsodont (high-crowned teeth that become lower crowned with older age because of wearing related to mastication which is not compensated by additional growth due to the closure of roots) and euhypsodont

Fig. 1 *Astegotherium dichotomus* (MMP 676-M): **a** general views of the fragmentary horizontal ramus and the associated osteoderms. Lateral view (above) and medial view (below, inverted) of the mandible. Osteoderms from right to left: one buckler osteoderm and two movable band osteoderms; **b, c** detail of **a** showing the lateral surface and the occlusal view of two molariform teeth; the dotted line separates enamel and dentine



(high-crowned teeth, in which growth continues all life without developing roots, and mastication abrasion is compensated by continuous growth) to replace hypsodont and hypselodont (respectively).

In this context, we prefer to use hypsodonta as a general term for high-crowned teeth (vs. brachyodont), whereas we use protohypsodont and euhypsodonty to indicate degrees of hypsodonty.

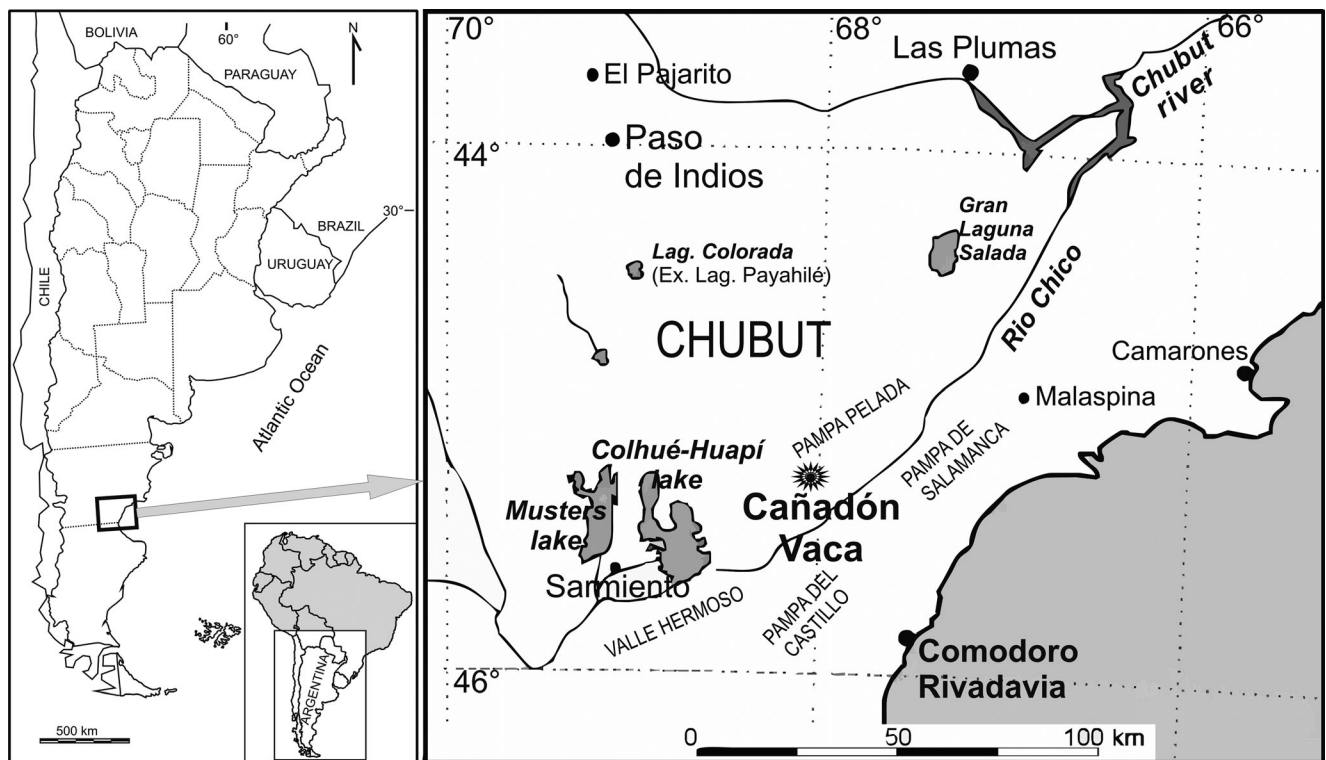


Fig. 2 Map showing the location of the Cañadón Vaca fossil locality in Patagonia, Argentina

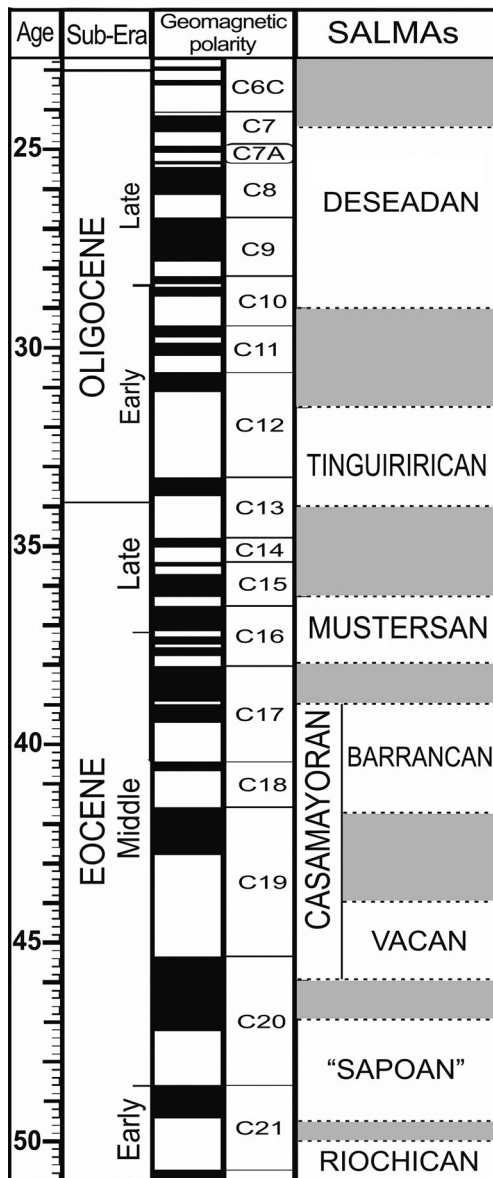


Fig. 3 Distribution of South American Land Mammal Ages (SALMAs) and magnetostratigraphy of the Paleogene in Patagonia (after Flynn et al. 2003; Ciancio et al. 2013; Dunn et al. 2013)

Description

The fragmentary horizontal ramus (probably left) bears three molariform teeth (mf). Dental measurements are (in millimeters): mfA 2.70 high, 2.80 long, and 2.10 wide; mfB 2.40 high, 2.70 long, and 2.10 wide; mfC 2.20 high, 2.60 long, and 2.00 wide (height refers to the exposed portion).

The mandibular body is elongated; the fragment is 14.5 mm long, 3.3 mm wide, and 5.9 mm high. It is convex in lateral view and flat in medial view, with a straight inferior margin. Alveoli corresponding to one tooth anterior to the three preserved molariforms and another tooth posterior to them can be observed. The mandible is low and slender, similar to those of other members of *Dasypodinae* (e.g.,

Dasypus and *Stegotherium*) and similar in size to that of *Dasypus novemcinctus* (Vizcaino 1994).

The molariforms are peg-like, oval in cross section, and with the greater axis oriented anteroposteriorly (Fig. 1a, b). The occlusal surface shows strong wear, a central crest, and a “double bevel”; i.e., a transversal ridge separates an anterior from a posterior surface which forms an angle between them in lateral view. The lingual and labial edges are high and coincide with the presence of an enamel layer in these areas. The molariforms are formed by dentine and present a thin enamel layer that partially covers the lingual and labial surface. These surfaces correspond to “nail-like” areas that extend from the apical edge across two thirds of the exposed height of the tooth; the enamel is restricted to those areas, and the remainder of the tooth is made up only of dentine (Fig. 1b, c). Cementum was absent in areas beyond the alveolus.

The molariforms are hypsodont: Their total height is greater than their width and length. There is no neck developed between exposed and intra-alveolar portions of the teeth. Two well-defined, closed roots are differentiated (Fig. 4a, b) and comprise the basal third of each tooth. The teeth show an extension of dentine below the enamel margin, forming the basal third of the exposed portion. The worn occlusal surface of the teeth lacks enamel; i.e., the primary occlusal surface is worn by use forming a secondary occlusal surface. These characteristics indicate that this dentition is hypsodont and more precisely protohypsodont (see discussion above). The individual was an adult, indicated by the closed roots, the absence of tooth (or tooth germ) below these teeth (as seen in Fig. 4a), and the size and morphology of the osteoderms (i.e., fully ossified bone, small follicles, large size).

Enamel microstructure *A. dichotomus* presents a thin enamel layer, approximately 60 μm thick in the transversal section measured at occlusal level (Fig. 5a). Despite the advanced tooth wear, the vertical section shows that the enamel layer extends over the apical two thirds of the tooth, and its thickness varies in apical-basal direction, decreasing toward the base of the tooth (Fig. 5e). The *schmelzmuster* consists of an inner zone of radial enamel and a very thin discontinuous outer prismless layer (PLEX), approximately 10 μm at its thickest (Fig. 5a). The prismatic enamel shows small and mostly rounded prisms arranged parallel to each other. Their diameter ranges between 3 and 4.5 μm . The prisms are separated by a thick interprismatic matrix (IPM) that becomes thicker toward the outer enamel surface (OES) and are surrounded by complete prism sheaths (Fig. 5c). In the vertical section, the prisms rise toward the outer surface at about 25°, but, toward the OES, the prisms change their course and became steeper. The IPM is arranged at 45° with respect to the prisms near the enamel-

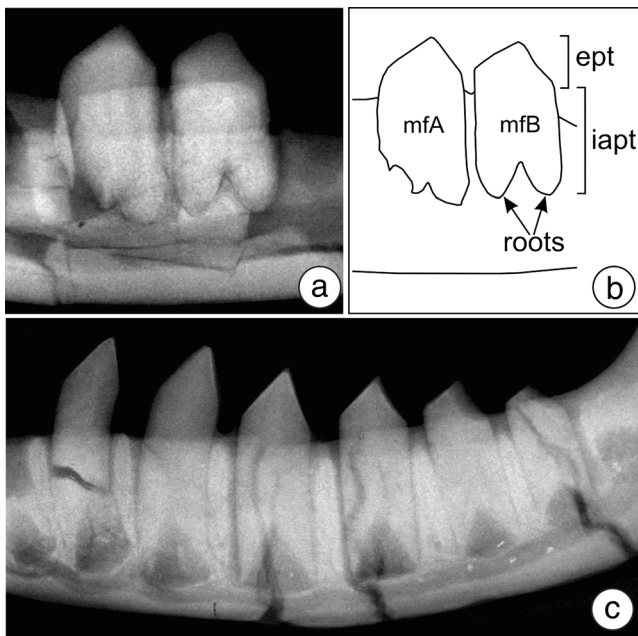


Fig. 4 **a** Radiograph of the mandibular fragment of *Astegotherium* showing the morphology of the intra-alveolar portions of *mfB* and *mfC*. **b** Linear representation of **a**. **c** Radiograph of the fragment of a mandible of *Utaetus buccatus* (MPEF PV 5426), showing the typical open-rooted morphology of dentine euhipodont teeth in xenarthrans. *ept* external portion of teeth, *iapt* intra-alveolar portions of teeth

dentine junction (EDJ) and is parallel to the prisms in the outermost enamel (Fig. 5d).

Dentine structure Xenarthrans possess a type of orthodentine with a different architecture compared to other mammals. It has a larger proportion of peritubular dentine, and the odontoblastic process shows frequent interconnections and an intensive branching of its extensions forming a complex meshwork, penetrating the intertubular dentine matrix (Kalthoff 2011). In some groups, two additional dentine types may differentiate: osteodentine and vasodentine. These tissues are very scarce or absent in other mammals (Kalthoff 2011). The molariforms of *A. dichotomus* are composed of only one type of dentine: orthodentine. Dentine tubules are evenly but quite widely spaced, and the dentine matrix is abundant. The diameter of the limits of the small lumen where the odontoblastic process sticks out varies between 1.3 and 1.8 μm (Fig. 5b). The orthodentine of *A. dichotomus* is similar to that described for *Utaetus* and *Octodontotherium* (Kalthoff 2011). We cannot measure the entire dentinal tubule because the true limits of the individual dentine tubules cannot be evaluated, which is possibly due to our preparation method.

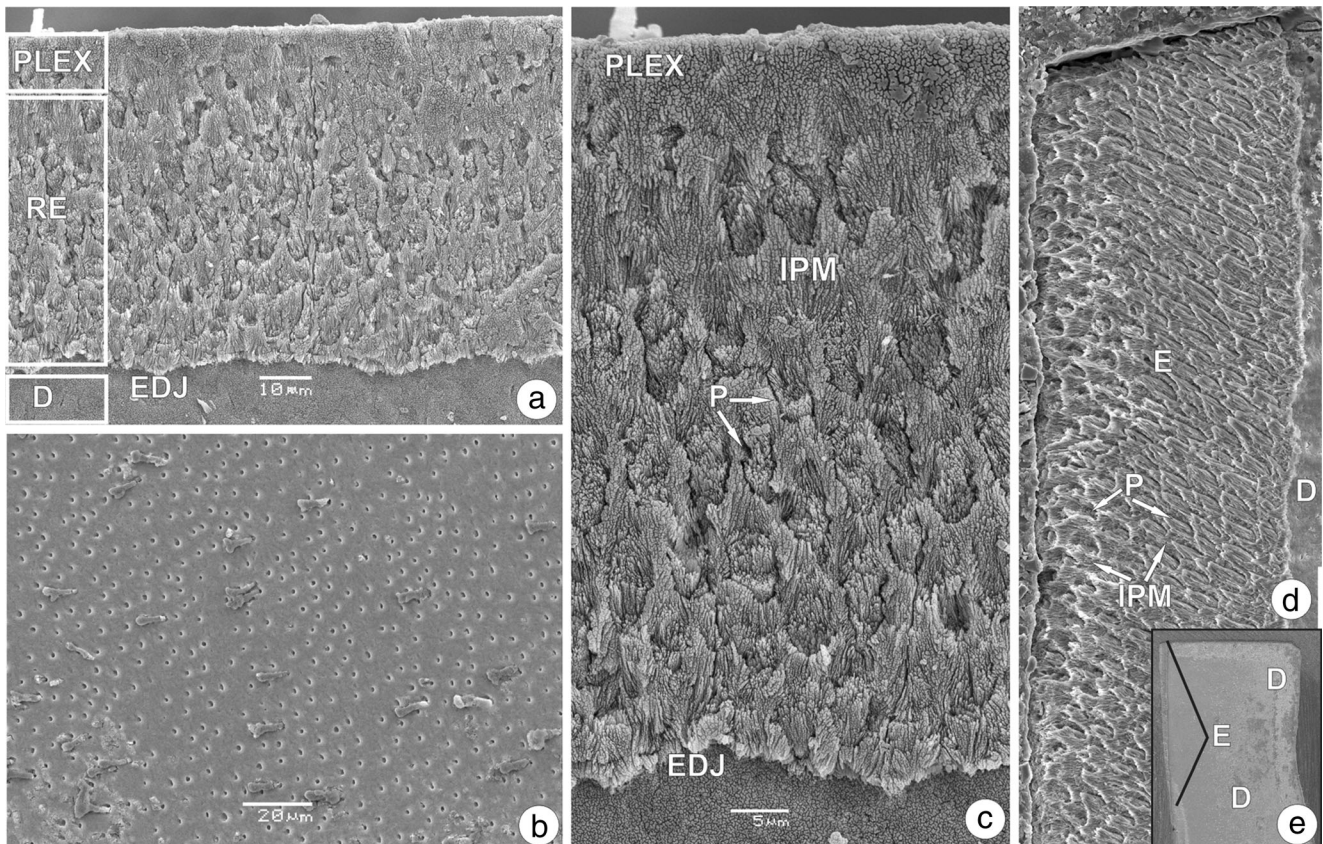


Fig. 5 Enamel and dentine microstructure of an *A. dichotomus* (MMP 676-M) tooth (*mfA*): **a** transversal section of enamel; **b** orthodentine microstructure in transversal section; **c** detail of **a**; **d** longitudinal section

of the enamel; **e** general view in longitudinal section showing the enamel. *E* enamel, *EDJ* enamel-dentine junction, *D* dentine, *IPM* interprismatic matrix, *P* prism, *PLEX* prismless enamel, *RE* radial enamel

Discussion

Loss of enamel in *Xenarthra* Enamel loss has occurred in several mammalian taxa across different clades (Wible et al. 2009; O'Leary et al. 2013). In *Xenarthra*, the entire clade is characterized by early reduction and loss of this dental tissue (Davit-Béal et al. 2009; Meredith et al. 2009). Nevertheless, the presence of enamel has previously been observed in cingulates (Fig. 6). Among extant species, a thin layer of enamel was observed in the apical portion on the unworn permanent molariforms of *Dasybus* species (Martin 1916; Ciancio et al. 2010). In fossils, true enamel has only been mentioned for the armadillo *U. buccatus* (Simpson 1932) from the late Middle Eocene of Patagonia, Barrancan subage of the Casamayoran SALMA, ca. 42–39 Ma (Ré et al. 2010; Dunn et al. 2013) (Fig. 3). In this case, the thin enamel layer is only on the labial and lingual sides of the molariforms. Its microstructure has never been illustrated, but according to its original description, it consists only of radial enamel (Simpson 1932). No enamel is present in adult specimens of *Utaetus* available to us (e.g., MPEF PV 5426; see Fig. 7.2 in Carlini et al. 2010). However, the specimen described by Simpson (1932, 1948) corresponds to a subadult (according to postcranial elements) with a

relictual enamel layer that would easily be lost with wear and consequently be absent in adult individuals. Unlike *Utaetus*, *Astegotherium* shows an enamel layer that extends to the vertical midpoint of the tooth, despite the fact that it is an adult individual with an advanced degree of wear.

As xenarthrans are clearly therian mammals, their common ancestor and/or fossil sister taxa possessed enamel. Meredith et al. (2009) studied the co-occurrence of dental morphological degeneration in the fossil record and molecular decay in the genome of several placental mammal orders. Their results, based on robust molecular data, suggest that the common ancestor of *Xenarthra* possessed teeth with enamel and that the loss of function of enamel-related genes occurred independently in the different major xenarthran lineages and even within the armadillo clade. Our data from the fossil record are congruent with this scenario and support a xenarthran common ancestor with enamel (Fig 7). Eocene armadillos such as *Utaetus* and *Astegotherium*, along with modern *Dasybus*, clearly demonstrate the presence of enamel in Cingulata. However, enamel has never been recorded in the remaining toothed *Xenarthra*, sloths (Tardigrada). Therefore, enamel loss has occurred independently in both clades (Cingulata and Pilosa) (Figs. 6 and 7).

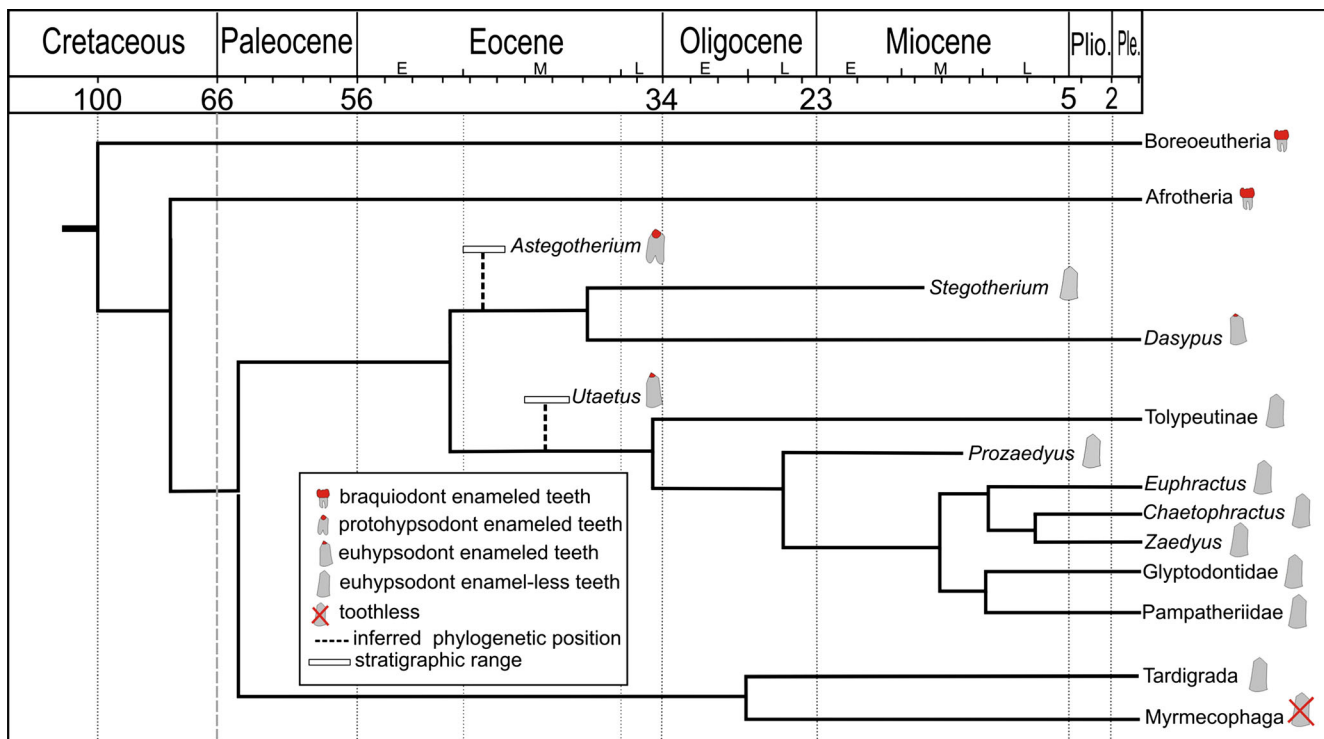


Fig. 6 Simplified phylogenetic relationship of fossil and extant xenarthrans mentioned in the text based on morphological and molecular results (Delsuc et al. 2012; Billet et al. 2011; Asher et al. 2009; Meredith et al. 2013). Phylogenetical position of *Astegotherium* and *Utaetus* was

inferred based on the literature and taxonomical position. The distribution of the characters related to hypsodonty and enamel in xenarthrans is shown. There are several remains that support that the origin of glyptodonts is earlier to what was inferred by the phylogenetic analysis

The presence of enamel in some xenarthrans shows that this feature is homoplastic. Homoplasy could be a result of either reversal or of independent evolution (convergence or parallelism) (Wake et al. 2011). In terms of parsimony, both interpretations may explain the character distribution. However, reversal is considered a controversial process because, commonly, once a complex organ is lost in evolution, it is not regained exactly in the original condition (Dollo's law) (DeSalle 2009; Meredith et al. 2009; Collin and Miglietta 2008). Therefore, we favor independent evolution to explain the repeated loss of enamel within xenarthrans.

Within Cingulata, enamel has been recorded in only one of the major groups (Dasypodidae), while in other groups (e.g., glyptodonts, pampatheres) enamel has never been reported. Enameled Eocene armadillos (*Astegotherium* and *Utaetus*) have never been included in large phylogenetic analyses, mainly because of the fragmentary condition of their remains. However, as mentioned before, *Astegotherium* (*Astegotheriini*) is accepted as a primitive Dasypodinae (Fig. 6). *Utaetus* has been considered to be related to the euphractins. Simpson (1948) noted similarities with *Prozadyus* (Euphractini, middle Miocene) and the *Zaedyus-Euphractus-Chaetophractus* group (Euphractini, Pliocene–recent). Hoffstetter (1958) mentioned that the structural pattern of the osteoderms of *Utaetus* is similar to that of the euphractins, whereas Rose (2006) considered that *Utaetus* resembles *Euphractus* based on some postcranial and dental characters. These resemblances led some authors to consider Utaetini Simpson, 1945 as a tribe of Euphractinae (Scillato-Yané 1980; McKenna and Bell 1997). Recently, Carlini et al. (2010) questioned the validity of Utaetini as a distinct tribe and suggested that it could be stem Euphractinae. Thus, based on the inferred divergence time of the Tolypeutinae–Euphractinae clade (ca. 33 Ma, sensu Delsuc et al. 2012) and on their primitive features, we estimate that *Utaetus* probably was an ancestor to the Euphractinae–Tolypeutinae clade. Besides, the Miocene tolypeutine *Pedrolypeutes* (from La Venta, Colombia) shows some postcranial features that suggest that tolypeutines may have originated from a generalized Euphractinae (Carlini et al. 1997). Thus, the enamel would have been lost independently in the main lineages traditionally recognized for Dasypodidae, euphractines–tolypeutines (including *Utaetus*) on the one hand and dasypodines (including *Astegotherium* and *Dasypus*) on the other (Fig. 7).

From an evolutionary perspective, the type of enamel described for *Astegotherium* (exclusively radial enamel, with prisms less than 5 μm and abundant interprismatic matrix) is plesiomorphic for Eutheria and would have

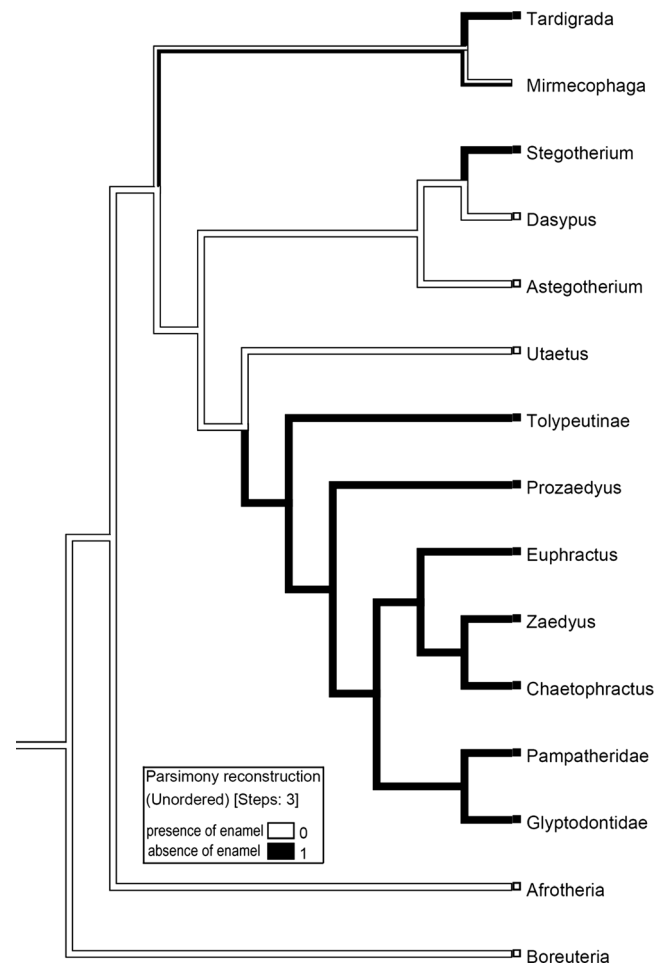


Fig. 7 Hypothetical reconstruction of the history of the loss of enamel in xenarthrans using maximum parsimony in Mesquite 2.72 (Maddison and Maddison 2009). The unordered binary character [presence of enamel: present (0) and absent (1)] was coded on the composite cladogram of Fig. 6. The topology of the cladogram is based on Delsuc et al. (2012), Billet et al. (2011), Asher et al. (2009), and Meredith et al. (2013), and the position of *Utaetus* and *Astegotherium* is inferred by taxonomical relationships

given rise to all other enamel types that occur in the clade (Wood and Stern 1997). This type of enamel is characteristic of numerous lineages of Mesozoic mammals and marsupials, and it may also occur in living placental groups such as scandentians, macroscelidids, paenungulates, dermopterans, and lipotyphlans (Wood and Stern 1997; Koenigswald 1997, 2000; Tabuce et al. 2007).

The primitive type of enamel for xenarthrans is still unknown. The new remains suggest two probable alternatives: (a) It would have been simple radial enamel, also present in the common ancestors of dasypodines and euphractines and (b) earlier xenarthrans possess multilayered enamel (or more advanced enamel types), and the

enamel microstructure of *Astegotherium* is secondarily plesiomorphic. Cingulates show a mosaic evolution for enamel reduction, given that the enamel of *U. buccatus* is more reduced and thinner than that of *A. dichotomus* and does not occur in adult specimens. Furthermore, in the living genus *Dasyypus*, the enamel layer is very thin and can only be observed in unworn permanent molars (Martin 1916; Ciancio et al. 2010). The reduction or loss of enamel could be associated with a change in the timing of relative growth during tooth development, for example, suppression of the stage of enamel formation and prolongation of dentine formation, as has been described for other mammals (Koenigswald 1993).

Hypsodonty in Xenarthra Hypsodonty has evolved independently in various mammal lineages, and it has been interpreted as an adaptation to the increased abrasive wear of the teeth, linked both to the increase of phytoliths formed by plants and to the increase of pyroclastic and sandy sediments in open environments, which deposit on (or between) the plants (Janis and Fortelius 1988; McNaughton et al. 1985; Scarano 2009). However, recent investigations have demonstrated that the phytoliths do not contribute too much to the dental microwear, and instead, exogenous grit and dust are the main cause (Sanson et al. 2007; Lucas et al. 2014).

In South America the first known mammal group to develop hypsodonty was Gondwanatheria (Koenigswald et al. 1999), followed by the archaeopithecids and archaeohyracids (Notoungulata) during the early Tertiary (Croft et al. 2003; Woodburne et al. 2014). Later, during the Eocene-Oligocene transition, hypsodonty became an important adaptation in the evolution of many herbivorous mammals in southern South America. Classically, acquisition of hypsodonty was correlated with the climatic changes occurring at that time which resulted in cooler and drier climates with more open habitats, i.e., woodlands to savannas (Kay et al. 1999; Koenigswald et al. 1999; Croft et al. 2003; Flynn et al. 2003; Ortiz-Jaureguizar and Cladera 2006; Scarano 2009). Recently, Strömberg et al. (2013) and Palazzesi and Barreda (2012) have proposed that the dominance of open habitats in Patagonia occurred during the Middle Miocene, more than 15 Ma later than previously inferred. Thus, grass dominance and openness of vegetation are not the main factor for the development of hypsodonty in South American mammals. Instead, exogenous grit (e.g., ash abundance), ingested along with food, would be a possible explanation (Madden 1999; Strömberg et al. 2013). An alternative or complementary cause for the early acquisition of hypsodonty in South American ungulates may be related to an increase in the chewing effort (Billet et al. 2009; Cassini and Vizcaíno 2012).

In the case of the xenarthrans, the evolutionary path of their hypsodonty is still unknown because the taxa known so far are characterized by the possession of definitive teeth that are both high crowned and open rooted, that is to say euhipodont (Mones 1982).

The development of hypsodonty in Xenarthra has been associated with the loss of enamel, which would result in greater tooth wear due to the lower mechanical resistance of dentine (Bargo et al. 2006; Vizcaíno 2009). Nevertheless, another factor that should be taken into account is the dental wear produced by external grit contamination incorporated into the food. The oldest known forelimb bones of xenarthrans (probably armadillos) show that they were able to dig burrows, as evidenced by their morphology, and they would have procured much of their food by digging, so they would ingest large amount of substrate particles (Berqvist et al. 2004; Vizcaíno 2009 and references therein). For mammals, eating while burrowing necessarily results in chewing a considerable amount of sediment that rapidly abrades the teeth; thus, fossorial mammals usually increase their tooth hypsodonty (Nevo 1979; Martin 1993).

Recently, Koenigswald (2011) defined hypsodonty on the basis of the development of different ontogenetic phases during early tooth development. In this context, xenarthrans have dentine hypsodonty, in which the teeth consist predominantly of dentine due to development of ontogenetic phase III (formation of the dentine-covered surface around the tooth), reduction or loss of phases I and II (primary occlusal surface characterized by the cusp in the apical portion of the unworn teeth and formation of enamel covered side walls, respectively), and suppression of phase IV (formation of roots), leading to euhipodonty. This type of hypsodonty differs from that of other placentals and is what Janis and Fortelius (1988) defined as “root hypselodonty.”

Euhipodonty could be considered as an extreme type of hypsodonty in which the tooth never stops growing and the formation of roots is indefinitely postponed (Koenigswald 1993). In particular, dentine hypsodonty could be characterized by suppression of crown development, so the resulting tooth is formed by dentine and/or the tissues that make up the root (Janis and Fortelius 1988; Koenigswald 2011). *A. dichotomus* already shows dentine hypsodonty, as shown by the extension of dentine below the enamel margin. However, unlike other xenarthrans, this specimen forms roots and may therefore be referred to as protohipodont, not euhipodont (Koenigswald 2011). The condition in *Astegotherium* represents a plesiomorphic stage relative to the typical and more derived condition that defines the remaining toothed Xenarthra (dentine euhipodonty), already present in *U. buccatus* (Fig. 4c).

The early development of dentine hypsodonty in the evolution of xenarthrans, together with the presence of

enamel, demonstrates that the acquisition of hypsodonty is at least partially uncoupled from the total loss of enamel. The acquisition of dentine euhypsodonty could have taken place in a short lapse of time at some point between the Middle Eocene, as suggested by the Middle Eocene age of *Astegotherium*, at least in later diverging dasypodines and probably in the rest of cingulates. The oldest known pilosan (*Pseudoglyptodon*, late Eocene–early Oligocene, see McKenna et al. 2006) also exhibits euhypsodonty. Notably, independent loss of enamel within dasypodids was predicted to have occurred close to this time period by the clock analysis applied by Meredith et al. (2009). Since the Late Eocene, fossil xenarthrans lack enamel; only members of the still-extant genus *Dasyurus* exhibit thin, apical enamel which disappears with wear early in postnatal ontogeny (Ciancio et al. 2010). This new perspective on the evolution of enamel and hypsodonty requires a reassessment of these characters in some fossils.

Reduction/loss of enamel, the acquisition of hypsodonty, and presence of peg-like teeth, supernumerary teeth, and interdental diastemata are dental specializations in several mammals adapted to a termitophagous diet (Charles et al. 2013). These features are shown in the oldest toothed mandible of an armadillo; hence, the dental morphology of basal armadillos would be an adaptation to this specific diet. Likewise, these inferences are based on comparisons with modern species. Further studies, such as microwear analyses (Green 2009), probably give us new evidence about the dietary habits of fossil armadillos and more information about which elements cause tooth wear.

Conclusions

We suggest that the ancestor of xenarthrans possessed enamel, supported by the presence in *Dasyurus*, *Astegotherium*, and *Utaetus* and parsimony reconstruction (Fig. 7). Like the predictions about the evolution of xenarthran enamel made by Meredith et al. (2009), this is also testable using the fossil record, in particular, once further remains are discovered of older cingulates such as *Riostegotherium* from Itaboraí. Craniodental remains of xenarthrans prior to the Eocene are not yet known but probably will be in the coming years.

The presence of orthodontine in *A. dichotomus* is similar to that described for other Paleogene xenarthrans and may be considered as primitive for the Xenarthra.

In the Xenarthra, hypsodonty has generally been associated with the loss of enamel. However, *Astegotherium* presents dentine hypsodonty with root formation and enamel present on much of each lateral wall, persisting well into adulthood. Thus, the primary development of hypsodonty

(protohypsodonty) in cingulates started before enamel loss, and the reduction or loss of enamel may have an influence on the subsequent development of euhypsodonty.

The acquisition of hypsodonty in cingulates (and in xenarthrans) was acquired independently of other Paleogene South American mammals, and factors influencing the evolution of hypsodonty could be related to the contamination of food items by abrasive particles ingested along with food.

Initial change from dentine protohypsodont teeth with enamel reduction to a dentine euhypsodont and enamel-less teeth resulted in a dental morphology common for post-Eocene xenarthrans. This basic dental morphology (dentine euhypsodonty without enamel, simple peg-like teeth, with orthodontine, probably associated with myrmecophagy) later became specialized secondarily in different cingulate lineages (e.g., lobulation of teeth and development of osteodentine as seen in glyptodonts and pampatheres) according to environmental influences and/or more specific food habits (i.e., omnivores, grazers, and browsers).

Astegotherium supports a recent hypothesis based on molecular data that enamel loss occurred independently not only within xenarthrans but also possibly within dasypodid armadillos. This study documents a compelling example of evolution leaving behind a common pattern in molecular and paleontological sources of data

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