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ORIGINAL PAPER

# Evolutionary Implications of Dental Eruption in *Dasypus* (Xenarthra)

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**Abstract** Late eruption of the permanent dentition was recently proposed as a shared anatomical feature of endemic African mammals (Afrotheria), with anecdotal reports indicating that it is also present in dasypodids (armadillos). In order to clarify this question, and address the possiblity that late eruption is shared by afrotherians and dasypodids, we quantified the eruption of permanent teeth in *Dasypus*, focusing on growth series of *D. hybridus* and *D. novemcinctus*. This genus is the only known xenarthran that retains two functional generations of teeth. Its adult dentition typically consists of eight upper and eight lower ever-growing (or euhypsodont) molariforms, with no premaxillary teeth. All but the posterior-most tooth are replaced, consistent with the identification of a single molar locus in each series. Comparison of dental replacement and skull metrics reveals that most specimens reach adult size with none or few erupted permanent teeth. This pattern of growth occurring prior to the full eruption of the dentition is similar to that observed in most afrotherians. The condition observed in *Dasypus* and many afrotherians differs from that of most other mammals, in which the permanent dentition erupts during (not after) growth, and is complete at or near the attainment of sexual maturity and adult body size. The suture closure sequence of basicranial and postcranial epiphyses does not correlate well with dental eruption. The basal phylogenetic position of the taxon within dasypodids suggests that diphyodonty and late dental replacement represent the condition of early xenarthrans. Additionally, the inferred reduction in the number of molars to a single locus and the multiplication of premolars represent rare features for any living mammal, but may represent apomorphic characters for *Dasypus*.

**Keywords** *Dasypus* · Teeth · Dentition · Replacement · Atlantogenata · Eruption

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## Introduction

Relative to other mammals, the peculiar dental morphology of Xenarthra is characterized by reduction and simplification (Engelmann 1978; McDonald 2003). Notably, the only xenarthran that retains two functional generations of teeth, as is common in other mammalian lineages, is the genus *Dasypus*. Most recent studies place *Dasypus* basal within cingulates, which are in turn the sister taxon to Pilosa (i.e., sloths and anteaters; see Delsuc et al. 2004; Gaudin and

Wible 2006). Among xenarthrans, Simpson (1932) noted the “absence or very feeble development of enamel in all recent and most extinct forms.” He summarized some reports regarding the presence of enamel in dasypodids by Tomes (1874) and Spurgin (1904), of an enamel-producing organ by Röse (1892), and of the absence of enamel in any stage of dasypodids by Ballowitz (1892). In contrast to the last result, Martin (1916) and Ciancio et al. (2010) confirmed the presence of enamel in *Dasypus*. Also, previous studies reported dental replacement in the fossil *D. punctatus* (Castro 2009) and the living *D. novemcinctus, D. hybridus* (Martin 1916), *D. kappleri* (Castro 2010), *D. yepesi*, and *D. sabanicola* (Castro et al. 2010).

Diphyodonty in *Dasypus* helps to establish hypotheses of dental homology. As the oldest fossil dasypodids already exhibited a modified dentition, the identification of tooth homologies is difficult. Based on embryology, shape, position, replacement, and presence of a diastema, Martin (1916) proposed I5-6 C1 P7 M1 as the dental formula of the lower jaw for *D. novemcinctus*, although some of those never erupt. Hoffstetter (1958) tentatively suggested the dental formula I1/2 C1/1 P4/4 M3/3 for the Dasypodidae.

Homologies of individual tooth loci do not seem to offer much information on the affinities of xenarthrans within mammals. However, late eruption of the permanent dentition has been argued to comprise a shared feature of at least some mammals endemic to southern continents (Asher et al. 2009). Anecdotal reports of late eruption of the permanent dentition among these clades include dasypodid xenarthrans (Hensel 1872; Martin 1916) and endemic South American notoungulates (Simpson 1967). Two very recent papers have quantified the latter (Agnolin and Chimento 2011; Billet and Martin 2011), but to date a quantitative analysis of dental eruption has not yet been published for dasypodids. Evidence for the late eruption of the permanent dentition in tenrecids and chrysochlorids dates to Leche (1907), and was recently proposed by Asher and Lehmann (2008) and Asher and Olbricht (2009) to be a synapomorphy for Afrotheria.

If present in *Dasypus*—the only living diphyodont xenarthran—late eruption may potentially comprise a shared anatomical feature of southern placental mammals, i.e., Afrotheria and Xenarthra grouped somewhat controversially in the clade Atlantogenata (Murphy et al. 2007). Here, we further scrutinize this possibility by quantifying eruption of the permanent dentition in a growth series of *Dasypus*, focusing on the species *D. hybridus* and *D. novemcinctus*.

## Methods

Measurements and quantification of dental and cranial proportions follow Asher and Olbricht (2009) (Fig. 1). As data on sexual maturity and absolute age during dental eruption in *Dasypus* are generally not available in scientific collections, we adopted size as an indicator of age, comparing the proportion of erupted permanent teeth with skull metrics. In addition, we recorded the state of epiphyseal fusion and cranial suture closure for each individual in order to evaluate the sequence of ossifications and to investigate possible correlates with body size and dental eruption. A given dental locus is referred as “erupted” when it exhibits at least some occlusal wear and reaches a similar horizontal plane as other teeth. In *Dasypus,* the deciduous precursor may frequently be lost during the osteological preparation. In most cases, tooth type (deciduous or permanent) was clearly determined by direct observation. In cases of uncertainty, we supplemented our diagnoses using radiographs (Fig. 2).


**Fig. 1** Skull and dentary of *Dasypus novemcinctus* (MLP 1-I-03-74) in ventral and lateral view, respectively, showing the measurements taken: **1** symphysis-condyle length; **2** palatal width at Mf8 (=M1?); **3** greatest skull length

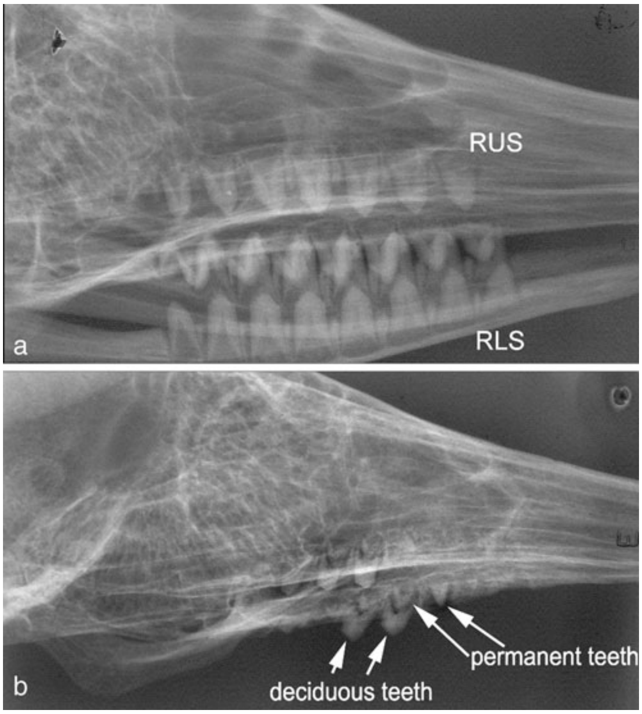


**Fig. 2** Radiographs of the skull of *Dasypus* adopted to determine status of dentition. **a** upper and lower permanent dentition of *D. novemcinctus* (MLP 2-III-00-14); **b** upper permanent dentition of *D. hybridus* (AAC-012), with some remaining deciduous precedents. "RUS" right upper series, "RLS" right lower series

We observed consistent replacement of all loci except the last upper and lower molariform. Thus, we infer the full dental formula of *Dasypus* to be seven upper and lower premolars followed by a single molar (see "Results"). Deviations from this formula are common (see Table 1). Individual teeth may be lost and resorbed in senescence, leaving no alveolus. In addition, some museum specimens lacked a dentary or maxilla. Therefore, the inferred complete dentition for a given individual may vary. To infer the ratio of proportion of erupted permanent teeth, we used as the numerator the number of observed permanent teeth, and as the denominator the maximum possible number of permanent teeth for that specimen, accounting for both loss of teeth in senescence and partial representation of a given individual in museum collections.

**Institutional Abbreviations**—**AAC**, Collection Alfredo A. Carlini at Museo de La Plata, La Plata, Argentina; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina.

**Anatomical Abbreviations**—M/m, upper and lower molar, respectively; Mf/mf, permanent upper and lower molariform, respectively; L/R, left and right, respectively; P/p, upper and lower premolar, respectively.

## Results

### Dental Homologies and Eruption Order

The adult dentition of *Dasypus* typically consists of 8/8 homogeneous, molariform teeth (Mf/mf), although many specimens have just seven with loss of the anterior-most locus. None of the upper teeth are placed in the premaxilla. The anterior seven loci in both the maxilla and dentary exhibit replacement, in contrast to the posterior-most tooth (Mf/mf 8) that erupts later and is not replaced (Fig. 3).

With respect to the morphology, the deciduous teeth are prismatic and double-rooted; their occlusal relief is an anterior-posterior bevel, with less worn labial and lingual borders. The permanent teeth are euhypsodont (ever-growing, high-crowned teeth, with an open pulp cavity, see Koenigswald et al. 1999; Koenigswald 2011), conical when first erupted, and become cylindrical with growth and wear. Before they are greatly worn, Mf/mf1 has a single cusp and Mf/mf2–Mf/mf7 exhibit a labial and a lingual cusp. Mf/mf8 differs in having two or three smaller cusps, with a circular rather than oval cross-section. The occlusion pattern between uppers and lowers alternates; i.e., a lower tooth occludes between its immediate upper homologue and its more anterior neighbor.

Based on these features, particularly the consistent lack of replacement at the Mf/mf8 locus, we infer that the bicuspate Mf/mf2–Mf/mf7 are premolars and Mf/mf8 is a molar. Because it shows a single cusp, Mf/mf1 may represent a canine. Alternatively, the occasional presence of a more anterior tooth, separated by a diastema in the maxilla (*D. yepesi*, MLP 30.III.90.2) and in the dentary (*D. novemcinctus*, MACN 49.460), yields nine rather than eight molariforms and may indicate that this additional element is a canine. The typical Mf/mf1 would then represent another premolar. At present we cannot rule out either possibility.

The order of dental eruption in *Dasypus* is variable. One specimen (MLP 30.III.90.2) shows a full complement of deciduous teeth, along with the erupted molar in each series. In contrast, another specimen (AAC 7) exhibits most upper and lower permanent premolars (P/p3-P/p7), but lacks fully erupted molars in the dentary, and shows an upper molar only on the left side. In some individuals (e.g., MLP 2.III.00.14) the molar fails to erupt on one side, without a sign of an alveolus. Otherwise, eruption of permanent dentition generally occurs from posterior to anterior, with upper and lower molars erupting first, followed by P/p 4-7 (e.g., AAC 12), then P/p3 (AAC 7), then P/p2 (MLP 3.X.14.3), then P/p1 (MLP 2.III.00.14).

### Osteological and Dental Correlates of Growth in *Dasypus*

In our sample, greatest skull length co-varies with dentary length. We used the latter measurement given its application in

**Table 1** Data on dental eruption, skull metrics, and suture closure in *Dasypus*

| Taxon | Museum | Adult teeth | Erupted/10 | Symph-cond | Prop adult dentary | PalWid M1 | GSL | Bs-Ps | Bs-Bo | Poscranial epiphyses | dist hum |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *D. hybridus* | MLP 1.I.03.69 | none | 0.00 | 52.60 | 0.941 | 10.7 | 67.3 | op | cl (sv) | op | cl |
| *D. hybridus* | MLP.1.I.03.67 | none | 0.00 | 51.80 | 0.927 | 11.9 | 65.7 | op | op | | |
| *D. hybridus* | MLP 22.II.00.9 | none | 0.00 | 45.20 | 0.809 | 10 | 59.2 | op | op | op | op |
| *D. hybridus* | MACN 33-11 | Lm1 | 0.33 | 50.60 | 0.905 | 11.3 | 64.9 | op | op | | |
| *D. hybridus* | MLP 1.I.03.65 | both lower molars | 0.63 | 54.10 | 0.968 | 12.3 | 68.2 | cl | cl (sv) | op | cl |
| *D. hybridus* | MLP 1.I.03.70 | both lower molars, no upper permanent teeth | 0.67 | 52.20 | 0.934 | 12 | 68.5 | op | op | op | op |
| *D. hybridus* | MACN 33-18 | R&LM1 | 0.67 | 49.20 | 0.880 | 10.5 | 63.4 | op | op | | |
| *D. hybridus* | MACN 33-16 | R&Lp1 | 0.71 | 48.20 | 0.862 | 10.8 | | | op | | |
| *D. hybridus* | MLP 3.X.94.3 | RM1;R&Lm1 | 0.97 | 51.30 | 0.918 | 12.1 | 65.5 | op | op | | |
| *D. hybridus* | MACN 32-178 | Rp5-6, Lp5, ?L&Rm1 | 1.25 | | | 10.7 | 64.8 | | | | |
| *D. hybridus* | AAC 12 | R&L M1 | 1.33 | | | 11.3 | 65.9 | | op | | |
| *D. hybridus* | MACN 33-19 | R&L P2,M1 | 2.86 | | | 11.2 | 63.8 | op | op | | |
| *D. hybridus* | MACN 33-176 | LP1-6, RP4-7; Rp4-5,Rp7,Rm1,Lp1, Lp4-7,Lm1 | 6.67 | 53.8 | 0.962 | 11.2 | | op | op | | |
| *D. hybridus* | MLP 16.IX.35.53 | R&L P1-P6,M1, R p1, p3-m1, L p4-p6,m1 | 6.88 | 53.5 | 0.957 | 11.1 | 69.5 | op | cl, (sv) | | |
| *D. hybridus* | AAC 7 | Rp3-p7,Lp3-p7, RP3-P7, LP3-P7,LM1 | 7.78 | 57.0 | 1.020 | 12.2 | 71.6 | cl | cl | | |
| *D. hybridus* | MLP 2.III.00.15 | R&L P2-P7, R p1-p6, L p1-p5,m1 | 8.89 | 58.5 | 1.047 | 11.2 | 74.8 | op | cl, (sv) | | |
| *D. hybridus* | MLP 869 | R&L P1-P7, R&L p1-p6 | 9.29 | 56.9 | 1.018 | 12 | 71.2 | op | cl, (sv) | op | cl |
| *D. hybridus* | MLP 868 | R&L P2-P6 R&L p1-p7, m1 | 9.33 | 54.8 | 0.980 | 11.7 | 70.0 | op | cl, (sv) | | |
| *D. hybridus* | MLP 16.IX.35.55 | R&L P1-P6, RM1, R&L p1-m1 | 9.38 | 58.5 | 1.047 | 10.6 | 74.0 | cl | cl, (sv) | | |
| *D. hybridus* | MLP 16.IX.35.48 | R&LP1-P6(Lower LP1-P6 RP1-P6 | 9.23 | 56.2 | 1.005 | 11.8 | 69.2 | op | cl, (sv) | | |
| *D. hybridus* | MACN 33-15 | R&L p1-7;R&LP1-7,RM1 | 9.38 | 45.7 | 0.818 | 10.5 | 61.0 | op | op | | |
| *D. hybridus* | MLP 1.I.03.71 | all permanent lower teeth with wear | 10.00 | 58.7 | 1.050 | 13.2 | 73.8 | cl | cl | | |
| *D. hybridus* | MLP 05.IX.97.03 | R&L P1-P7, R&L p1-p7 | 10.00 | 56.6 | 1.013 | 11.7 | 70.7 | op | cl, (sv) | op | cl |
| *D. hybridus* | MLP 16.IX.35.54 | all permanent teeth with wear | 10.00 | 58.4 | 1.045 | 11.6 | 74.3 | cl | cl, (sv) | | |
| *D. hybridus* | MLP 4.VIII.98.10 | all permanent teeth with wear | 10.00 | 54.7 | 0.979 | 11.2 | 68.6 | op | cl, (sv) | op | op |
| *D. hybridus* | MACN 30-17 | R&L P1-6; R&L p1-7,m1 | 10.00 | 55.4 | 0.991 | 11.7 | 70.2 | cl, (sv) | cl, (sv) | | |
| *D. hybridus* | MACN 13220 | RP2-7,M1,LP3-7,M1;Rp1-7,Lp1-7,m1 | 10.00 | 54.4 | 0.973 | 11.7 | 68.3 | cl | cl | | |
| *D. hybridus* | MACN 13900 | R&LP1-7,R&Lp1-m1 | 10.00 | 55.9 | 1.000 | 11.2 | 70.7 | op | cl | | |
| *D. hybridus* | MACN 54-156 | R&LP2-M1,R&Lp1-m1 | 10.00 | 61.0 | 1.091 | 11.9 | 76.6 | cl | cl | | |
| *D. hybridus* | MACN 36-980 | R&LP1-6,Lp1-m1,Rp1-7 | 10.00 | 58.1 | 1.039 | 11.7 | 73.4 | | cl | | |
| *D. hybridus* | MACN 30-18 | R&LP1-6,Lp1-6,Rp1-m1 | 10.00 | 52.0 | 0.930 | 11.5 | 65.0 | cl | cl | | |
| *D. hybridus* | MACN 32-174 | Lp1-m1 | 10.00 | 54.0 | 0.966 | | | | | | |

**Table 1** (continued)

| Taxon | Museum | Adult teeth | Erupted/10 | Symph-cond | Prop adult dentary | PalWid M1 | GSL | Bs-Ps | Bs-Bo | Poscranial epiphyses | dist hum |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *D. novemcinctus* | MACN 49-460 | none | 0.00 | 55.4 | 0.703 | 11.7 | 73.7 | op | op | | |
| *D. novemcinctus* | MLP 1.I.0374 | R&L M1, R&L m1 | 1.18 | 77.8 | 0.987 | 14.5 | 99.4 | cl | cl, (sv) | | |
| *D. novemcinctus* | MACN 39-459 | R&Lm1 | 1.25 | 71.4 | 0.906 | | | | | | |
| *D. novemcinctus* | MACN 39-465 | R&Lm1 | 1.25 | 75.4 | 0.957 | 14.6 | | op | op | | |
| *D. novemcinctus* | MACN 51-33 | R&L M1, R&L p1,m1 | 1.94 | 68.0 | 0.863 | 14.1 | 85.2 | op | op | | |
| *D. novemcinctus* | MACN 49-391 | R&LP1-2,P4-M1; Lp1-5,m1; Rp1-6,m1 | 8.44 | 82.1 | 1.042 | 16.5 | 103.7 | cl, (sv) | cl | | |
| *D. novemcinctus* | MLP 1.I.03.76 | R&L P1-P6, RM1, R&L p1-m1 | 9.06 | 66.7 | 0.846 | 13.9 | 86.1 | op | cl, (sv) | op | op |
| *D. novemcinctus* | MLP 2.III.00.14 | R&LP1-P7, RM1, R&Lp1-p7, Lm1 | 9.68 | 62.8 | 0.797 | 12 | 80.0 | op | op | | |
| *D. novemcinctus* | MACN 49-350 | R&LP1-M1, Lp1-m1, Rp1-2, p4-m1 | 9.69 | 82.6 | 1.048 | 17 | 101.4 | cl | cl | | |
| *D. novemcinctus* | MLP 5.V.99.3 | all permanent lower teeth with wear | 10.00 | 76.4 | 0.970 | | | | | | |
| *D. novemcinctus* | MLP 8.IV.98.2 | all permanent teeth with wear | 10.00 | 78.3 | 0.994 | 15.3 | 102.6 | cl | cl | | |
| *D. novemcinctus* | MLP 1.I.03.73 | all permanent teeth with wear | 10.00 | 76.1 | 0.966 | 14.3 | 94.4 | op | cl | cl | cl |
| *D. novemcinctus* | MLP 1.I.03.72 | all permanent teeth with wear | 10.00 | 77.0 | 0.977 | 15.2 | 96.8 | cl | cl | cl | cl |
| *D. novemcinctus* | MLP 1.I.03.75 | all permanent teeth with wear | 10.00 | 69.2 | 0.878 | 14.7 | 90.8 | op | op | | |
| *D. novemcinctus* | MLP 2.X.02.1 | all permanent teeth with wear | 10.00 | 79.6 | 1.010 | 15.4 | 96.7 | op | cl | cl | cl |
| *D. novemcinctus* | MLP 1750 | all permanent teeth with wear | 10.00 | 80.8 | 1.025 | 14.9 | 101.4 | cl | cl | | |
| *D. novemcinctus* | MACN 49-383 | L&Rp1-m1; L&R P1-7 | 10.00 | 83.9 | 1.065 | 15.9 | 103.8 | cl, (sv) | cl | | |
| *D. novemcinctus* | MACN 49-458 | R&LP1-M1, R&Lp1-m1 | 10.00 | 82.4 | 1.046 | 15.5 | 101.3 | op | op | | |
| *D. novemcinctus* | MACN C.04750 | RP1-M1,LP1,P3-M1;R&Lp1-m1 | 10.00 | 79.3 | 1.006 | 15.1 | 97.4 | cl | cl | | |
| *D. novemcinctus* | MACN 50-123 | R&LP2-M1, R&Lp1-m1 | 10.00 | 75.3 | 0.956 | 16 | 92.7 | cl, (sv) | cl | | |
| *D. novemcinctus* | MACN 39-461 | R&LP1-M1 | 10.00 | 77.6 | 0.985 | 16 | 100.9 | cl | cl | | |
| *D. novemcinctus* | MACN 49-397 | RP1-6,LP1-7;L&R p1-m1 | 10.00 | 83.9 | 1.065 | 17.5 | 103.5 | cl | cl | | |
| *D. novemcinctus* | MACN 33-92 | Rp1-m1 | 10.00 | 87.5 | 1.110 | | | | | | |
| *D. sabanicola* | MLP 22.II.00.6 | R&Lp1-m1; R&LP1-P4 | 8.28 | 56.6 | | 13.4 | 71.1 | | cl | | |
| *D. septemcincctus* | MLP 1.II.03.64 | R&Lp1-m1, R&L P1-P6 | 9.33 | 53.8 | | 11.6 | 69.2 | | op | op | op |
| *D. yepesi* | MLP 30.III.90.2 | m1,M1 | 0.63 | 55.1 | | 12 | 71.3 | | op | | |

"Erupted/10" indicates the number of completely erupted permanent teeth, taken as a proportion out of ten (see "Methods"); "symph-cond" shows the symphysis-condyle length, "Proportion adult dentary" shows the symphysis-condyle length of each specimen divided by the median dentary length of adult specimens as defined by the presence of a worn and fully erupted permanent dentition (55.9 mm in *D. hybridus*; 78.8 mm in *D. novemcinctus*), "PalWid M1" shows the palatal width at M1, "GSL" indicates greatest skull length, "Bs-Ps" basisphenoid-presphenoid suture, "Bs-Bo" basisphenoid-basioccipital suture, "op" open, "cl" closed, "(sv)" suture visible. Postcranial sutures (distal ulna, proximal and distal humerus, distal tibia, distal femur, acetabulum) varied together, except for the distal humerus (dist hum). All values given in millimeters (mm)

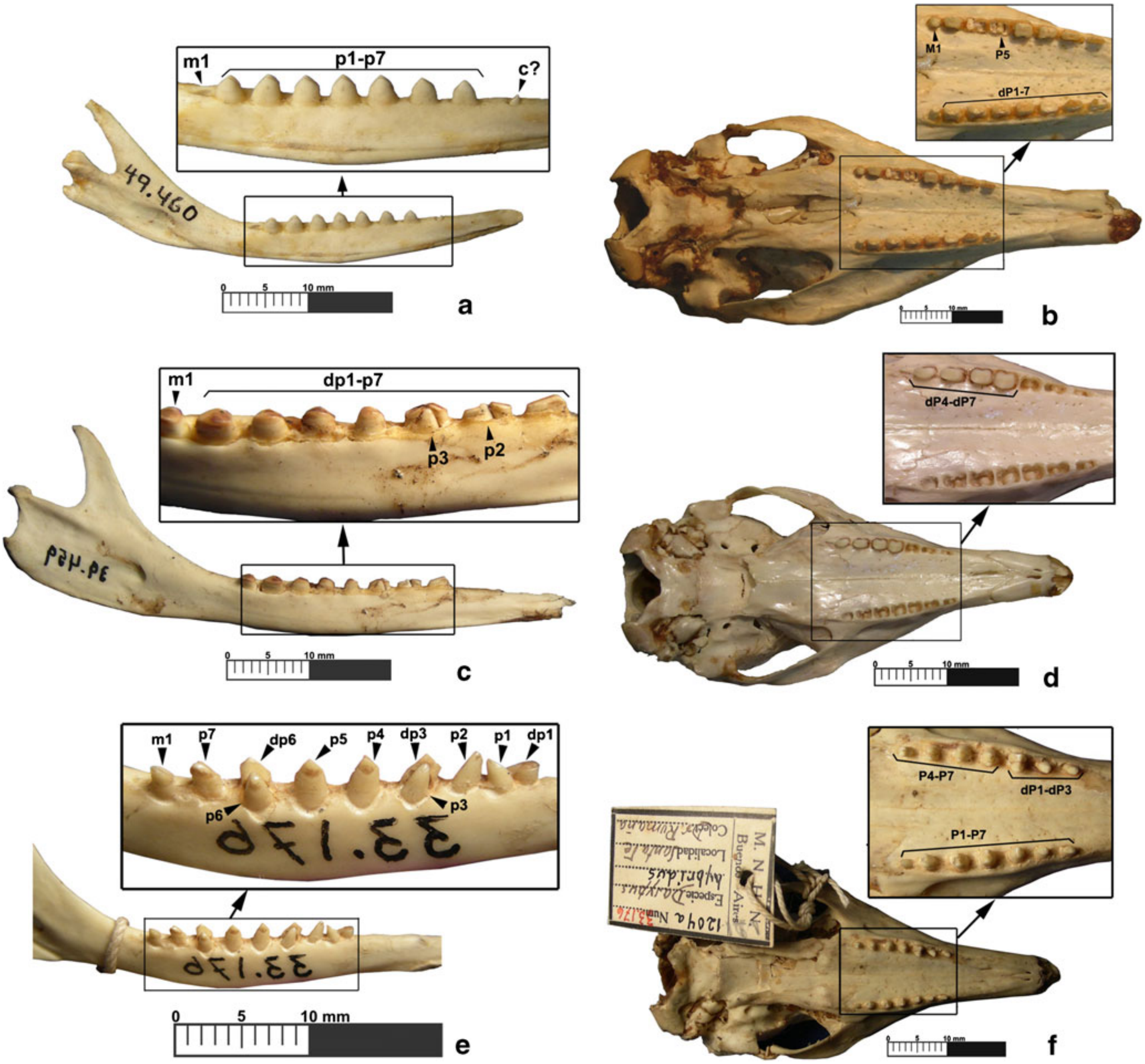


**Fig. 3** Dentition of *Dasypus* in different phases of replacement. **a** *D. novemcinctus*, MACN 49-460; **b** *D. novemcinctus*, MLP 1-I-03-74; **c** *D. novemcinctus*, MACN 39-459; **d** *D. hybridus*, MLP 1-I- 03-67; **e**, **f** *D. hybridus*, MACN 33-176. Images **c** and **e** are reversed. c?, probably canine; dP/dp, deciduous premolars; P/p, premolars; M/m, molars

previous studies (e.g., Asher and Olbricht 2009). The correlation between both measurements allows comparison with previous studies (e.g., Wetzel and Mondolfi 1979; Wetzel 1985; Stangl et al. 1995) that instead sampled cranial length for adult specimens. The palatal width at the M1 level showed a weaker correlation with both dentary and skull length in our sample.

To establish adult age in armadillos, previous authors used the fusion of the basioccipital-basisphenoid suture (Wetzel and Mondolfi 1979; Wetzel 1985). Furthermore, Stangl et al. (1995) distinguished young adults on the basis of a closed basioccipital-basisphenoid suture, open basisphenoid-presphenoid suture, and a fully erupted permanent dentition; they recognized old adults when both basicranial sutures were obliterated. However, our results indicate that these criteria, along with dental eruption order, show considerable variation. For example, 38% of specimens with closed basisphenoid-basioccipital sutures (e.g., MLP 1. I.03.65), and 31% specimen with both basicranial sutures closed (e.g., MLP 1.I.03.74), have an incompletely erupted permanent dentition (Table 1, Fig. 3). On the other hand, all *D. hybridus* and all but two *D. novemcinctus* (MLP 1.I.03.75

and MACN 49-458) with a fully erupted permanent dentition show a closed basioccipital-basisphenoid suture.

The sequence of suture closure in *Dasypus* shows that the basicranium starts fusion prior to the union of epiphyses in postcranial elements. There are differences in the timing between basicranial sutures: the basioccipital-basisphenoid closes earlier than basisphenoid-presphenoid (e.g., MLP 1.I.03.69). Also, in *D. hybridus*, the distal humerus closes before the basisphenoid-presphenoid suture, which remains open even in one of the largest individuals (MLP 2.III.00.15). Our sample of *D. hybridus* does not contain individuals with a fused distal ulna, proximal humerus, distal femur, distal femur, or acetabulum. In *D. novemcinctus*, the basisphenoid-presphenoid suture closes after fusion of the humerus and other long bone epiphyses.

Comparison of dental replacement and skull metrics (Fig. 4, Table 1) reveals that *Dasypus* approaches adult size with none (e.g., *D. hybridus*, MLP 1.I.03.69, 94% of median adult dentary size) or few (e.g., *D. novemcinctus*, MLP 1.I.03.74, 99% of median adult dentary size showing only M/m1) erupted permanent teeth.

Specimens of *D. hybridus* with completely erupted permanent dentitions have a dentary length of 52.0–58.7 mm (median=55.9, *N*=11) and greatest skull length of 65.0–76.6 mm (median=68.6, *N*=11). The latter measurement agrees with the greatest skull length (GSL) obtained by Wetzel and Mondolfi (1979), 66.3–75.5 mm (mean=70.2; *N*=26). Specimens of *D. novemcinctus* with a completely erupted permanent dentition show a dentary length of 69.2–87.5 mm (median=78.8, *N*=14) and greatest skull length of 90.8–103.8 mm (median=94.7, *N*=12). For the latter species, the wider range of GSL (78.7–110.9) presented by Wetzel and Mondolfi (1979) also encompasses the greatest skull length (97.1–107.3) obtained by Stangl et al. (1995).

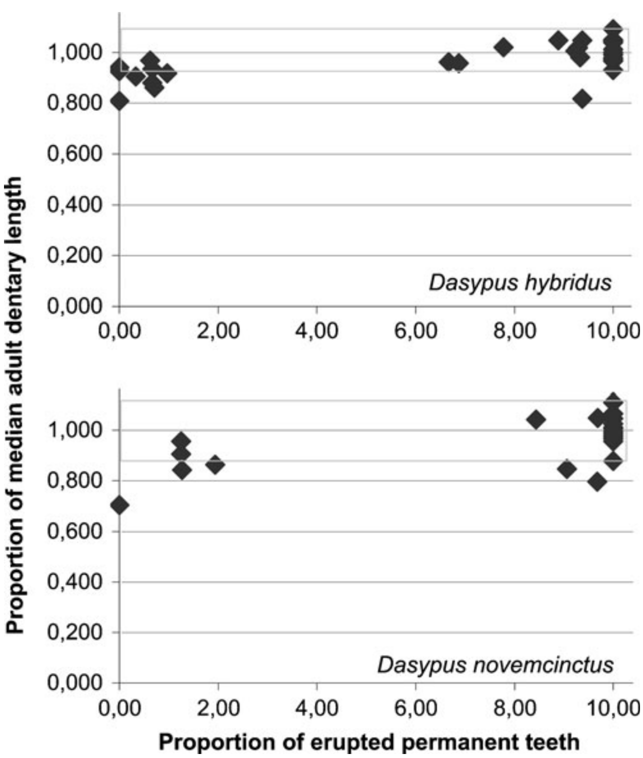


**Fig. 4** Proportion of adult dentary length (y-axis, median value=1.0) in relation to the proportion of erupted permanent teeth (x-axis, all permanent teeth erupted=10.0) for the specimens of *Dasypus hybridus* and *Dasypus novemcinctus* provided in Table 1. Gray boxes within each graphic represent range of dentary length in specimens with all permanent teeth erupted. Note high frequency of adult-sized dentaries among specimens with incompletely erupted teeth

## Discussion

The comparison of dental replacement and the dentary metrics in *D. novemcinctus* and *D. hybridus* indicates that they reach adult size having few erupted permanent teeth (Fig. 4), and that most cranial growth in these species takes place prior to the full eruption of the permanent dentition. Assuming size as a proxy of age, combined with data from other mammals in which growth and dental eruption are largely coincident (Asher and Olbricht 2009), we conclude that *Dasypus* shows relatively late eruption of its permanent teeth, as previously observed in afrotherians (Asher and Lehmann 2008).

Considering the basal position of *Dasypus* within Dasypodidae (Delsuc et al. 2004; Gaudin and Wible 2006; Möller-Krull et al. 2007), and the dental replacement patterns of mammals generally (van Nievelt and Smith 2005), it is reasonable to conclude that both diphyodonty and late dental replacement represent the ancestral condition of early xenarthrans. Given the unique status among living mammals of the reduction in the number of molars to a single locus and the multiplication of premolars, it is more difficult to estimate the polarity of these features relative to the xenarthran common ancestor, but they may represent apomorphic characters of *Dasypus*.

We find that most long bone epiphyses remain unfused in adult-sized specimens in our sample of *D. hybridus*, except for the distal humerus, which is closed in our largest specimens. In *D. novemcinctus*, long bone epiphyses throughout the skeleton fuse in our largest (and presumably oldest) specimens. In both species, the basioccipital-basisphenoid suture tends to fuse prior to postcranial epiphyses. The sequence of epiphyseal closure in *Dasypus* shows little resolution and a low correlation with dental eruption in our sample. For this reason, the use of the basicranial sutures to assign age is not appropriate, especially for young adults. The identification of features that allow an accurate determination of skeletal age in armadillos is a matter that requires further study.

The delayed eruption observed in *Dasypus* differs from that of most other mammals in which the adult dentition is generally fully erupted at or near the attainment of sexual maturity and adult body size. As noted by Asher et al. (2009), delayed eruption occurs in some non-afrotherian mammals (e.g., artiodactyls), but may still optimize as a synapomorphy for southern placental mammals. Given the basal position of *Dasypus* within Xenarthra, and the presumption that its dentition is representative of that of the xenarthran common ancestor, our results support late dental eruption as a shared feature of Xenarthra and Afrotheria (see Asher et al. 2009), recognized as a clade of southern placental mammals (Atlantogenata) based on molecular data (Hallström et al. 2007; Murphy et al. 2007; Prasad et al. 2008). Other possible morphological synapomorphies of Atlantogenata are worth further investigation.

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