Mamm. biol. **66** (2001) 193–203
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http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Supernumerary molars in neotropical opossums (Didelphimorphia, Didelphidae)

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Receipt of Ms. 17. 05. 2000
Acceptance of Ms. 28. 09. 2000

Abstract

Dental abnormalities, such as the occurrence of extra teeth, are recurrently found in many groups of mammals. Supernumeray molars were found in *Didelphis aurita*, *D. albiventris*, *D. marsupialis*, *Philander andersoni*, *P. frenata*, *P. opossum*, *Chironectes minimus*, and *Caluromys philander*. Frequencies of occurrence of supernumerary teeth in these marsupial species remained within a range similar to that found in other species. Four hypotheses are proposed and discussed to explain the origin of these teeth: appearance of extra teeth due to excessive development in size of the skull, reappearance of an atavistic condition, retention of the third deciduous premolar at the eruption of the permanent premolar, or some sort of ontogenetic disturbance that lead to the duplication of a tooth germ. The first hypothesis is discarded as all individuals have normal sizes for the species. No evidence in the marsupial fossil record supports the second. The morphology of the teeth observed does not support the third, as all teeth are apparently permanent (except for one specimen). Finally it is hard to find evidence against or in favour of the fourth, as there is no information available of the development of the museum specimens observed.

Key words: Marsupials, abnormalities, dentition, Neotropics

Introduction

The study of abnormalities can be particularly interesting for those involved in developmental genetics and morphological evolution, providing useful data for medical, evolutionary, and taxonomic studies. For instance, by focusing on abnormalities one can assess the potentialities for the rise of new variant morphologies. Morphological shifts occur with the rise of such deviant morphologies and its spreading through the taxon. Thus, abnormalities, as highly deviant morphologies, could initiate such morphological shifts.

Mammal dental abnormalities have long been reported, and include teeth specific malformations (e. g. Long and Long 1965; Feldhamer and Stober 1993), size reduction or missing of teeth (e. g. Mech et al. 1970; Drehmer and Ferigolo 1996), or supernumerary teeth (e. g. Krutzsch 1953; Steele and Parama 1979; Kvam 1985; Drehmer and Ferigolo 1996). The latter corresponds to the occurrence of more teeth than those expected from the species normal dental formula. Such phenomenon

1616-5047/01/66/04-193 $ 15.00/0.

has been described for eutherian families as diverse as e. g. Mustelidae (Long and Long 1965), Otariidae (Drehmer and Ferigolo 1996), Felidae (Kvam 1985), Canidae (van Valen 1964), Cervidae (Fowle and Passmore 1948; Pekelharing 1968; Steele and Parama 1979; Mech et al. 1970), Soricidae (Hooper 1946), Dipodidae (Krutzch 1953), and Sciuridae (Goodwin 1998). Within the marsupial family Didelphidae supernumerary teeth have been reported for the genus *Didelphis* (Allen 1901; Takahashi 1974) only and recently for *Philander* (Hershkovitz 1997). The aim of this study therefore is to investigate the situation for South American marsupials in more detail.

Material and methods

The following species were investigated: *Caluromys philander* (Linnaeus, 1758), *Chironectes minimus* (Zimmermann, 1780), *Didelphis albiventris* Lund, 1840, *D. aurita* Wied-Neuwied, 1826, *D. marsupialis* Linnaeus, 1758, *Philander andersoni* (Osgood, 1913), *P. frenata* (Olfers, 1818), and *P. opossum* (Linnaeus, 1758), from specimens deposited in the following collections: Museu Nacional, Rio de Janeiro (MN); Departamento de Zoologia, Universidade Federal de Minas Gerais (DZUFMG); Museu de Zoologia, Universidade de São Paulo (MZUSP); American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); National Museum of Natural History (NMNH); and Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro (MC). Collection numbers, sexes and localities for specimens found with supernumerary molars are listed in table 1.

Unless otherwise specified tooth morphology nomenclature follows Reig et al. (1987). Notations in super- or subscript refer to specific (upper or lower, respectively) tooth rows, as traditionally used in tooth formulae nomenclature (*e. g.* M^4), but when no specific row is meant, we chose not to use super- or subscript (*e. g.* M4).

Results

Frequency of occurrence

The frequency of supernumerary molars occurrence in each of the investigated species was calculated based on adult specimens with four molars erupted, as the number of individuals presenting any extra tooth divided by the total number of specimens examined for that species. The frequency of supernumerary teeth is 0.7% (1/141) in *C. minimus*; 1.2% (1/82) in *C. philander*; 0.5% (3/655) in *D. albiventris*; 0.3% (1/337) in *D. aurita*; 1.0% (9/872) in *D. marsupialis*; 2.8% (1/36) in *P. andersoni*; 0.8% (2/244) in *P. frenata*; and 0.3% (2/767) in *P. opossum*.

Tooth morphology and position

The location of the supernumerary tooth found is reported in table 1. Supernumerary teeth were found at all molar rows; however, they were more frequent at the upper rows.

Caluromys philander

The only specimen (MZUSP 11591) found with an extra tooth presents it at the end of the right inferior molar series (Fig. 1). It is slightly smaller than the M4. Cuspids are distinguishable with the protoconid excessively developed in comparison to the paraconid and metaconid that are reduced. The talonid is slightly reduced, and is divided antero-posteriorly by a crest, not present in the normal teeth, that creates two basins and makes the identification of the talonid cusps more difficult. This tooth is aligned with the molar series in occlusal view, but its crown is slightly tilted to the lingual side.

Chironectes minimus

The only occurrence of a supernumerary molar for this species (MZUSP 16545) is an extra molar erupting behind the right M_4 (Fig. 2). The tooth is not fully erupted (only the protoconid, and the tips of the metaconid and entoconid emerge from the bone), but its crown pattern is clearly visible and identifiable with conids and cristids pattern identical to the M_4. The tooth is clumped, as there is no space available for it in the mandibular ramus and is erupting

Table 1. Individuals observed with supernumerary teeth, with respective species, museum number, sex, locality of origin and location of supernumerary molars. Legend: M: Male; F: Female; UL: Upper left row; UR: Upper right row; LL: Lower left row; LR: Lower right row. Museum acronyms as in text

Species	Museum Number	Sex	Locality	Location of supernumerary molar			
Caluromys philander	MZUSP 11591	M	Fordlândia, Pará, Brasil		UR		
Chironectes minimus	MZUSP 16545	F	Cametá, Pará, Brasil				LR
Didelphis albiventris	AMNH 63852	M	Utcuyacu, Junin, Perú			LL	LR
Didelphis albiventris	DZUFMG 120	M	Santa Luzia, Minas Gerais, Brasil		UR		
Didelphis albiventris	MN 22250	F	Brasília, Distrito Federal, Brasil	UL	UR	LL	LR
Didelphis aurita	AMNH 133034	M	Paraiba do Sul, Rio de Janeiro, Brasil	UL	UR		
Didelphis marsupialis	AMNH 33243	M	Esmeraldas, Ecuador		UR		
Didelphis marsupialis	AMNH 93978	F	Norte do Rio Amazonas, Faro, Pará, Brasil				LR
Didelphis marsupialis	AMNH 95345	M	Rio Tapajós, Igarapé Amorim, Pará, Brasil				LR
Didelphis marsupialis	AMNH 95361	M	Rio Tapajós, Inajatuba, Pará, Brasil		UR		
Didelphis marsupialis	AMNH 209179	M	Beni, Bolivia	UL	UR	LL	LR
Didelphis marsupialis	USNM 280966	M	Villanueva, Colombia		UR		
Didelphis marsupialis	USNM 51092	M	Rio Tapajós, Caxiricatuba, Pará, Brasil		UR		LR
Didelphis marsupialis	USNM 545457	F	Belém, Pará, Brasil		UR		
Didelphis marsupialis	FMNH 22199	M	Sierra de Mérida, Mérida, Venezuela	UL			
Philander andersoni	AMNH 72017	F	Rio Curaray, Loreto, Perú	UL			
Philander frenata	MC 267	M	Maricá, Rio de Janeiro, Brasil	UL	UR		
Philander frenata	MN 5769	M	Santa Teresa, Espírito Santo, Brasil	UL	UR		
Philander opossum	AMNH 34373	?	Bagadó, Chocó, Colombia	UL	UR		
Philander opossum	USNM 337643	M	El Recreo, Zelaya, Nicaragua	UL	UR		

with its crown tilted about 45 degrees lingual and anteriorly in comparison to the remaining molars.

Didelphis albiventris

Specimen DZUFMG 120 presents a single supernumerary molar, erupted behind the right M^4 (Fig. 3). It is a small tooth (approx. 1/3 of the size of the normal M^4), with an oval crown, with two cusps connected by cristae. Its reduced size and abnormal crown shape makes it difficult to identify what these cusps and cristae are equivalent to in normal teeth. The tooth is very tight, as there is no place for it on the maxilla, behind the M^4. The crown of this tooth is approximately in the same occlusal plane as normal molars, but it does not occlude with any inferior tooth.

Specimen MN 22250 possesses one supernumerary molar at the end of each series. The extra tooth on the left superior series is smaller than the M^4 and similar in shape, yet with much reduced stylar cusp C, and slightly compressed, so that the stylar cusp E (metastyle) is closer to the paracone than in the M^4. All remaining cusps are clearly identifiable. It is also slightly rotated counter-clockwise. Its crown lies beneath the occlusal plane of the rest of the series but occludes with the extra molar of the inferior series. The extra tooth on the right superior side is identical in shape to the M^4, and of about half its size. Unlike the tooth previously described, orientation and cusps are similar to the M^4, and apart from the size difference, there is no deformation or other shape difference. Its crown also lies beneath the occlusal plane of the M^4, and apparently does not occlude. The left inferior extra tooth (Fig. 4) is overall similar to the M_4, especially the trigonid is identical to the M_4 trigonid, with all cusps identifiable. In the talonid, however, the hypoconulid is closer to the hypoconid, giving the whole talonid a more elongated or triangular shape. Finally, the supernumerary molar on the right mandible (Fig. 5) also presents a trigonid identical to the M_4 trigonid, but with a slightly different talonid, with a hypoconulid somewhat farther from the trigonid than in the latter.

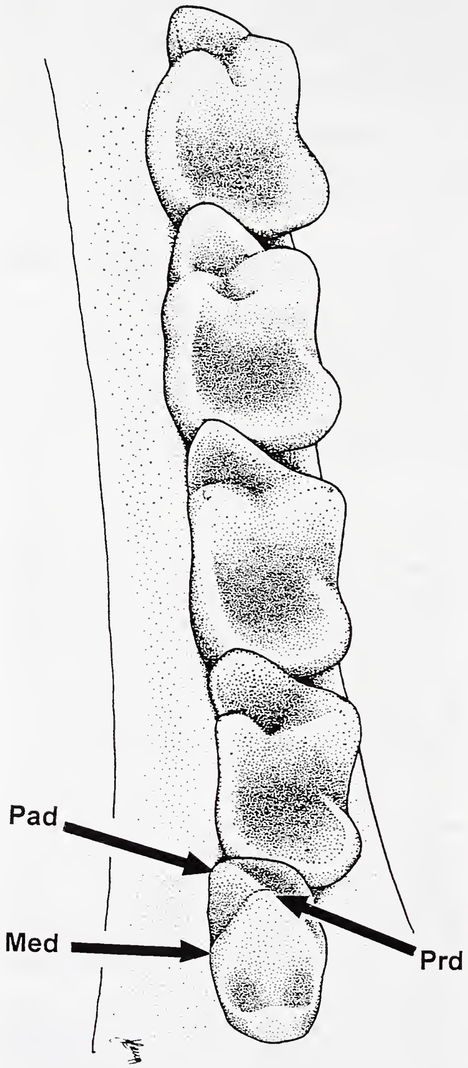

Fig. 1. Right inferior molar series of *Caluromys philander* (MZUSP 11591), with a supernumerary molar (arrow). Occlusal view. Protoconid (Prd), paraconid (Pad), metaconid (Med).

Didelphis aurita

Specimen AMNH 133034 possesses one supernumerary molar in each side of the superior row. Both extra teeth have a molariform shape but are slightly reduced. The extra tooth on the right superior series is posteriorly directed, probably due to the lack of space in the row, and is not at the oclusal plane of the remaining teeth. Its cusps are present and distinguishable with a crown pattern resembling a normal M^4. The other extra tooth at the left superior series is not at the occlusal plane of the remaining row and its cusps, although distinguishable, do not resemble a normal M^4 pattern.

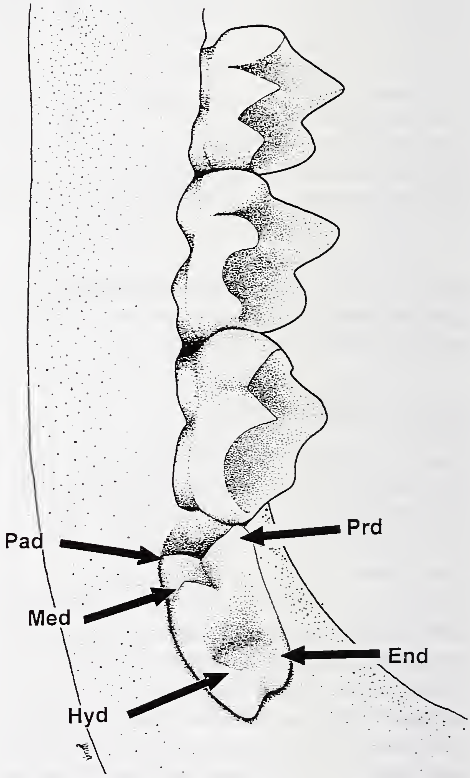

Fig. 2. Right inferior molar series (M2–M4) of *Chironectes minimus* (MZUSP 16545), with a supernumerary molar (arrow), viewed from the occlusal plane of the extra tooth. Protoconid (Prd), paraconid (Pad), metaconid (Med), entoconid (End), hypoconid (Hyd).

D. marsupialis

Specimen AMNH 93978 possesses one extra tooth on each side of the superior rows. Both are reduced but with a molariform shape. The extra teeth at the right has some cusps visible (but hardly identifiable), and a crista, which is apparently the centrocrista, oriented with the antero-posterior axis of the skull.

Philander frenata

Specimen MC 267 presents one extra molar on each side, at the end of the upper molar series. On the left side (Fig. 6), the supernumerary tooth is smaller than the M^4. Some cusps are discernible, as well as what appears to be the centrocrista. Protocone, paracone and metacone are identifiable, but the cusp present on the opposite side

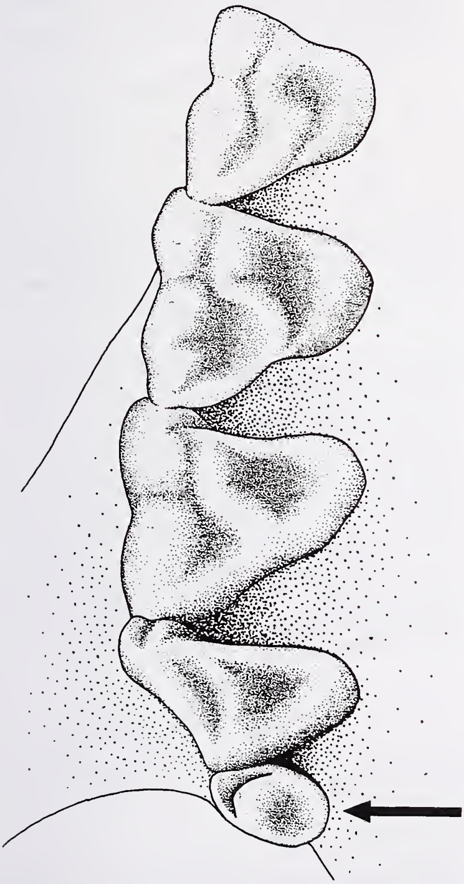

Fig. 3. Right superior molar series of *Didelphis albiventris* (DZUFMG 120), with a supernumerary molar (arrow). Occlusal view.

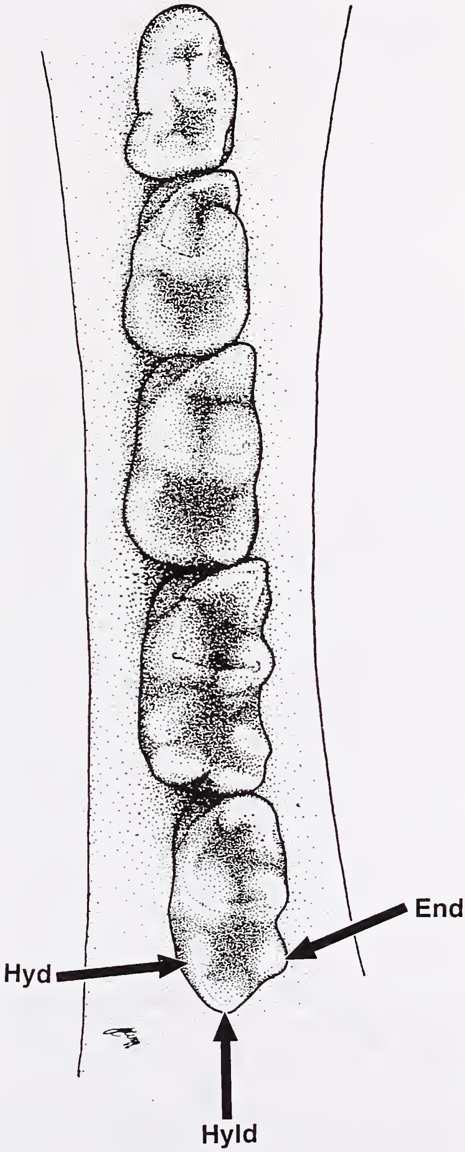

Fig. 4. Left inferior molar series of *Didelphis albiventris* (MN 22250), with a supernumerary molar (arrow). Occlusal view. Entoconid (End), hypoconid (Hyd), hypoconulid (Hyld).

of the centrocrista cannot be identified. Actually, this extra tooth resembles a normal M^4 as described by HERSHKOVITZ (1997) for *Philander*, and the M^4 resembles a normal M^3: On the right side the extra tooth is more deformed, somewhat ovally shaped with some cusps visible (but hardly identifiable), and a partially formed crista (apparently the centrocrista, oriented with the antero-posterior axis of the skull). Unlike on the left side, the right tooth shows some degree of wear on the cusps and outer cristae. In both cases teeth are partially cluttered on the M^4, and crowns are on a different occlusal plane than the remaining molars (roots are more developed).

Specimen MN 5769 also presents one extra molar on each side, behind the upper left and right M^4. On the right side (Fig. 7), the extra molar is partially erupted. It is dislocated, due to the lack of space on the den-

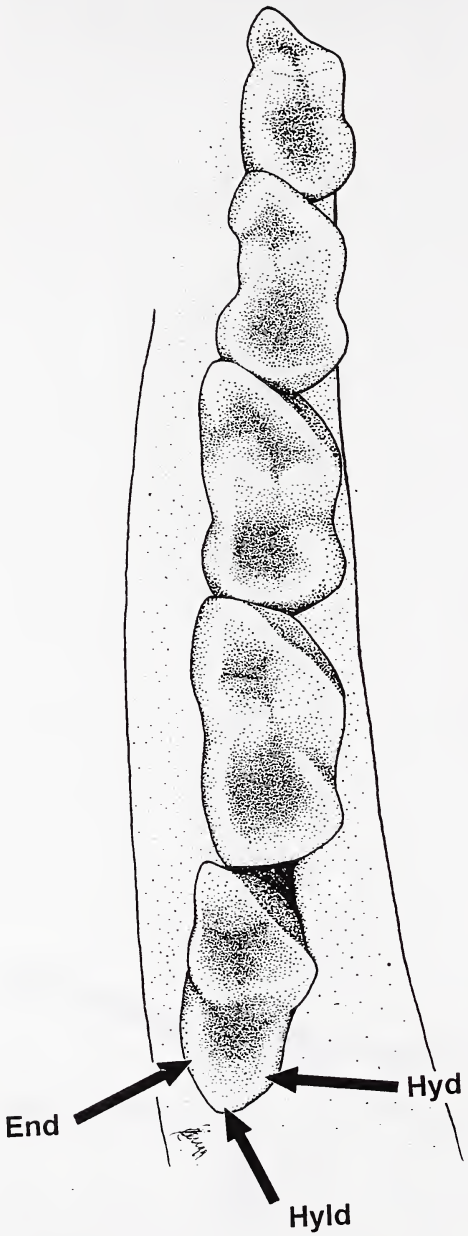

Fig. 5. Right inferior molar series of *Didelphis albiventris* (MN 22250), with a supernumerary molar (arrow). Occlusal view. Entoconid (End), hypoconid (Hyd), hypoconulid (Hyld).

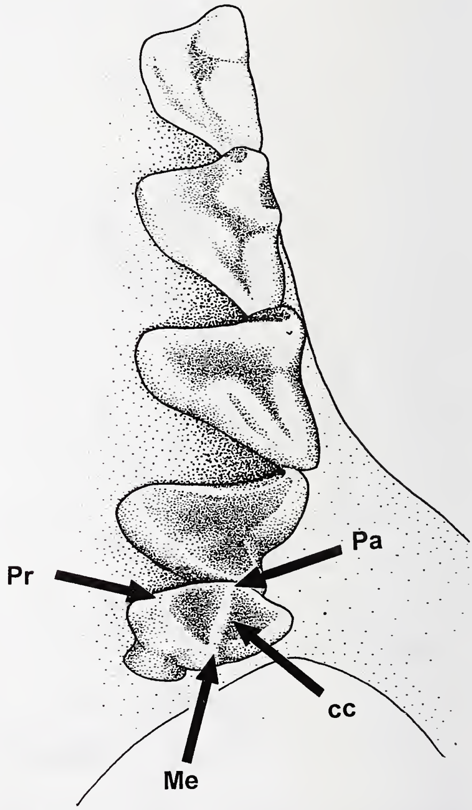

Fig. 6. Left superior molar series of *Philander frenata* (MC 267), with a supernumerary molar (arrow). Occlusal view. Protocone (Pr), paracone (Pa), metacone (Me), centrocrista (Cc).

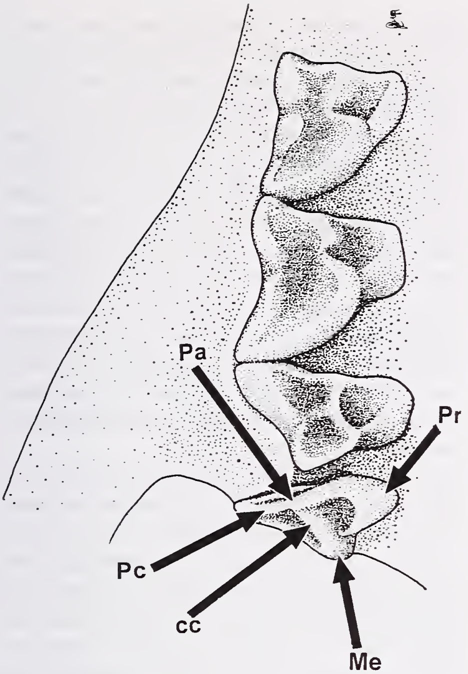

Fig. 7. Right superior molar series of *Philander frenata* (MN 5769), with a supernumerary molar (arrow). Occlusal view. Protocone (Pr), paracone (Pa), metacone (Me), centrocrista (Cc), paracrista (Pc).

tary behind the M^4, with its occlusal plane of the tooth posteriorly directed. A centrocrista is also recognisable, as well as protocone, paracone and metacone. The paracrista is also present, and the tooth lacks stylar cusps C, D and E. On the left side. the extra tooth is more oddly formed, with a crown of ovoid shape. Cusps are perceptible, such as an inner crista, probably the centrocrista. The occlusal plane, however, is aligned with the remaining molars of the series.

P. opossum

One specimen (AMNH 34373) presented a single supernumerary tooth at the end of each superior row. The extra tooth at the left side is reduced, but otherwise much similar to a normal M^4 in cusp patterns. It is also at the same occlusal plane of the remaining teeth. The extra tooth at the right superior side is occluding anteriorly oriented, and seems to be pushing forward the row. It is reduced, with distinguishable cusps.

Discussion

The occurrence of dental abnormalities such as supernumerary teeth is a rare and unpredictable phenomenon that makes the study of its specific developmental causes and processes very unlikely. Although the alternative explanations to the supernumerary teeth phenomenon are not always exclusive we provide a critical evaluation of some possible explanations.

Altough rare, the frequencies of supernumerary molars reported here for the Didelphidae fall within the range of those found in other mammal (placental) groups where the phenomenon has been reported (e.g. 1.6% (9/550) in European lynxes (*Lynx lynx* (Linnaeus, 1758)) Kvam 1985; 0.2% (1/580) in red deers. (*Cervus elaphus* Linnaeus, 1758) and 0.8% (1/130) in wapitis (*Cervus canadensis* Linnaeus, 1758) Pekelharing 1968; 3.7% (4/109) in mooses (*Alces alces* (Linnaeus, 1758)), Steele and Parama 1979.

First it is important to consider if these supernumerary teeth are a return to a lost primitive condition, thus being an atavistic character. For instance, Takahashi (1974) suggested that the presence of supernumerary incisors is an atavistic character of some *Didelphis* specimens. However, Berkovitz (1978) states that no more than five incisor tooth germs were ever observed in *Didelphis*. Thus, the supernumerary incisors studied by Takahashi (1974) doubtfully can be interpreted as atavistic characters. Furthermore, an atavistic explanation presents some limitations in our case, as the basic marsupial dental formula, exhibited by extant Didelphidae ($I^5_4C^1_1P^3_3M^4_4$) differs from the basic therian formula at the time of metatherian divergence from eutheria by the lost of premolar teeth on the former (Barbour 1977). Besides the proposition of some authors that the third deciduous premolars (dP3) could in fact be first molars and the subsequent molars being M2 to

M5 (e.g. Hershkovitz 1992), there is no mention of a truly additional fifth molar in marsupials (living or fossil). The only known exception would be the Australian numbat *Myrmecobius fasciatus* Waterhouse, 1836 (Myrmecobiidae), which can present 5 or 6 molars (Thenius 1989). In this case however, it is believed that the molar number is a secondary specialisation resulting from jaw elongation and not related to any ancestral condition, or primitive trait. Hence, an atavistic explanation could be advanced for a possible supernumerary premolar but not for molars. In fact there is no fossil record relating the occurrence of five molars in marsupials.

Another hypothesis relates an excessive size development to the emergence of an extra tooth at the end of the tooth row. However, as all specimens studied here presented standard sizes for their species, such a hypothesis does not seem to be the case. Furthermore, as we reported, in many cases there is actually a lack of space for these teeth to develop, which however did not prevent the teeth from appearing and the amount of space available does not seem to be related to the completeness of the tooth formation.

In some reports the occurrence of supernumerary teeth had been related to developmental disorders, such as splitting of the tooth germ (Krutzch 1953; Long and Long 1965; Pekelharing 1968; Steele and Parama 1979). These developmental alterations on the embryonic germ will likely lead to an incomplete development of one or both duplicated teeth, as observed in cervids, and in some cases resulting in an extra tooth "mirrored" in relation to the original one (Pekelharing 1968). The supernumerary molars here reported vary from morphological perfect M^4-like teeth to very small vestigial teeth, and never in this "mirrored" situation. In fact, no clear association between lack of space and amount of development of the supernumerary tooth could be found. Furthermore, knowledge on precise tooth development for most of these species is not existant, and all individuals examined are field caught, making an exact determination of the underlying phenomenon hard. Nevertheless, some sort of random developmental disorder could be an explanation for many of the cases we studied here.

Such an explanation is more difficult to accept in extreme cases such as MN 22250 and AMNH 209179, where four almost fully developed molars are present, requiring a simultaneous event of germ duplication in all M4. A genetically based disturbance with simple mendelian inheritance is also unlikely, as one of the specimens studied (MC 267) was field caught but maintained alive for captive breeding, and none of the offspring presented any similar phenomenon.

An alternative explanation could be that the premolariform P3 had erupted without loss of the molariform dP3. If this is the case, the cheek teeth observed would in fact be, in order: P1, P2, P3, dP3, M1, M2, M3 and M4. The eruption of the P3 would displace the whole molar series (at the time of eruption of the P3, only M1 and M2 are present), thus forcing the M3 and M4 to the end of the maxillar bone, which in case of lack of space could explain the deformations eventually observed. According to Berkovitz (1978), in *Didelphis virginiana* the third premolar develops in the embryonic dental lamina between the second premolar and the deciduous molar. Thus, if the deciduous molar was displaced posteriorly instead of falling, the sequence of the teeth after eruption would be the one previously stated. However, both upper and lower deciduous premolars are morphologically different from first permanent molars; dP^3's are narrower than M^1's, and dP_3's have narrower trigonids than M_1's, and their talonids are bigger in relation to the trigonid than in the M_1. In all animals examined here the first molar in the series has all characteristics of an actual M1, and not of a dP3, which denies this hypothesis.

The different shape variations observed in these teeth can be explained by the classic field model of mammalian heterodonty. This model postulates that heterodonty derived by the existence of three morphogenetic fields (incisor, canine, and molar).

These fields determine what the final form of a developing tooth bud will be (BUTLER 1939) but conflicting functional aspects are also important. In the genus *Peromyscus* Gloger, 1841, for instance, correlations among cheekteeth make M^3 and M_3 widths somewhat independent (VAN VALEN 1962). The characteristics of each type of teeth appear early in tooth ontogeny although initial buds are undifferentiated (ARCHER 1974; BERKOVITZ 1978; BUTLER 1978). At weaning *Didelphis* has three functional molariform teeth. As it grows the deciduous premolar (which is molariform) is shed at the same time of the eruption of M3 (TRIBE 1990). In this sense the deciduous P3's would actually be molars because when they grow they are located in a molar field (ARCHER 1974). Allometric growth of the bones changes the fields causing the so-called deciduous premolar to be shed and substituted by the P3's now growing in a premolariform field. Different allometric rates among taxa would then explain the differences in ontogeny of dentition among didelphids observed by TRIBE (1990) and us (ASTÚA DE MORAES and LEMOS, unpubl. data).

Apparently it is possible that ancestors of metatherians had two dentitions like the placentals, since some secondary incisive and canine buds appear but are resorbed later in *Antechinus flavipes* (Waterhouse, 1838) (ARCHER 1974). Thus the dental lamina of the oral epithelium seems to have the potentiality to develop more teeth buds than teeth that effectively erupt. The supernumerary teeth could then be a congenital accidental anomaly. The resorption of the buds may be determined by the fixation of the teeth above them. With available space above buds (lack of teeth), these buds would develop into supernumerary teeth. In fact, supernumerary incisives and molars are more frequent (being the only ones so far described) because there is the available space in the diastema, between incisives and canines and also behind the cheek teeth row. Supernumerary incisives appear on the premaxillary bone only (TAKAHASHI 1974). The additional teeth usually show the characteristic morphology of the teeth of the region where they appear, Exceptions are valid in cases when where there is no space for the tooth to fully develop into its normal morphology. Thus, varied morphology can be expected to appear.

Regardless of an explanation these dental abnormalities do not seem to be especially selectively disadvantageous, as all animals reached adulthood before being captured.

Acknowledgements

We are grateful to G. A. B. FONSECA (DZUFMG), A. L. GARDNER (USNM), L. F. B. OLIVEIRA, and L. O. SALLES (MN), B. PATTERSON (FMNH), M. DE VIVO (MZUSP), and R. VOSS (AMNH) for access to the collections under their care. To M. A. R. MELLO and LENA GEISE for translation and corrections in the Zusammenfassung. ARIANNA CAMARDELLA gave us precious help sharing her knowledge on didelphid molar morphology, as well as J. A. W. KIRSCH regarding dental formulas in *Myrmecobius*. JAIR DA SILVA did the drawings. We thank two anonymous referees for suggestions. The work was partially supported by grants from CNPq, FAPERJ, FAPESP, FUJB, PROBIO/MMA and PRONEX.

Zusammenfassung

Überzählige Molaren bei neotropischen Beuteltieren (Didelphimorphia, Didelphidae)

Abweichungen von der arttypischen Zahnzahl wie das Auftreten zusätzlicher Zähne, werden in vielen placentalen Säugetiergruppen gefunden. Die Untersuchungen an neotropischen Beuteltieren haben ebenfalls überzählige Molaren ergeben bei: *Didelphis aurita*, *D. albiventris*, *D. marsupialis*, *Philander opossum*, *P. frenata*, *P. andersoni*, *Chironectes minimus* und *Caluromys philander*. Die Häufigkeit des Auftretens überzähliger Zähne bei diesen Arten bleiben innerhalb eines Bereiches, der ähnlich demjenigen bei anderen Arten ist. Folgende Möglichkeiten zur Deutung dieses Phänomens

werden erwogen: 1) Erscheinung der Extrazähne als Folge einer übermäßigen Entwicklung der Schädelgröße; 2) Atavismus; 3) Persistenz des dritten Milchprämolaren bei Erscheinen des Dauerzahnes; 4) Wachstumsstörungen, die zur Verdoppelung eines Zahnkeimes führen. Die erste Hypothese wird verworfen, da alle Einzelindividuen eine arttypische Größe haben. Kein fossiler Hinweis unterstützt auch die zweite. Die Morphologie der beobachteten Zähne unterstützt auch die dritte nicht, da es sich um Zähne des Dauergebisses handelt. Schließlich ist es schwierig, Beweise gegen oder zugunsten der vierten Hypothese zu finden, da keine Informationen vorhanden sind, über die Entwicklung der Zähne bei den bearbeiteten Museumsexemplaren.

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