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Dental anomalies in *Caluromys* (Marsupialia, Didelphimorphia, Didelphidae, Caluromyinae) and a reassessment of malformations in New World marsupials (Didelphimorphia, Microbiotheria and Paucituberculata)

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Abstract: Dental anomalies have been documented in almost all mammalian orders, and include supernumerary or missing teeth, teeth with aberrant occlusal surfaces and/or roots and teeth in unusual positions. Our objectives were the description and categorization of dental anomalies in all species of the genus *Caluromys*. We studied 462 crania, recorded and classified dental anomalies in four categories: variations in occlusal/root morphology; teeth in unusual positions; supernumerary/missing teeth; presence of unshed deciduous premolars. We found anomalies in all species, with a percentage ranging from 11% to 6.3%. *Caluromys derbianus* produced anomalous M4/m4 and flipped crowns, the other two species produced higher numbers of missing teeth. We infer that flipped crowns might have consequences in mastication, while other anomalies seem to be less functionally important, especially those at the end of the toothrow. Comparisons with other New World marsupials show caluromyines have more anomalies in M4/m4 shape (similar to microbiotherids) and flipped crowns, while didelphids have more supernumerary teeth, and caenolestids have more missing teeth.

Keywords: dental symmetry; mammal teeth; woolly opossums.

Introduction

Mammal teeth are an efficient system to capture, hold, fracture and fragment food, which is essential to meet the physiological demands needed to sustain higher energy intakes (Ungar 2010). Teeth occlusion and mastication are thus important features involved in food processing. In this context, dental anomalies in mammals are not frequent due to their negative effect on occlusion and mastication (Wolsan 1984, Martin 2007).

The presence of dental anomalies has been documented in almost all mammalian orders, extant or fossil (e.g. Wilson 1955, Wolsan 1984, Miles and Grigson 1990, Martin 2007, Arnal and Vucetich 2011, González Ruiz et al. 2015). These anomalies could be of different type and include supernumerary or missing teeth, teeth with aberrant occlusal surfaces and/or roots, and teeth in unusual positions (Miles and Grigson 1990). Within mammals, dental anomalies in marsupials have been registered anecdotally in different species by Bensley (1903, 1906), Osgood (1921, 1924) and González (2000). Further comparative studies were made by Archer (1975) for Australian marsupials, and by Astúa de Moraes et al. (2001), Martin (2007, 2013), and Chemisquy and Martin (2016) for South American species, while Miles and Grigson (1990) quantified and described dental anomalies for several genera of marsupials, especially from Australia.

Living marsupials are found in Australia and some adjacent islands, and the Americas from southern Canada to southern Argentina. They live in a variety of environments and have different diets, from carnivorous to herbivorous, and their teeth vary accordingly. New World marsupials are divided in three orders: (1) the highly speciose and broadly distributed Didelphimorphia, commonly known as opossums, which have a basic tribosphenic molar morphology, and are included in different feeding categories (Chemisquy et al. 2015, Goin et al. 2016); (2) the pseudo-diprotodont Paucituberculata, commonly known as shrew-opossums, which are restricted to Andean environments of western South America, have procumbent lower incisors and quadritubercular upper molars, and have a predominantly animalivorous diet (Ungar 2010, Martin 2013, Patterson 2015, Goin et al. 2016); and (3) the *monito del monte*, the only living species of the order Microbiotheria which lives in the subantarctic forests of Argentina and Chile, and has a frugivorous/animalivorous diet (Amico and Aizen 2000,

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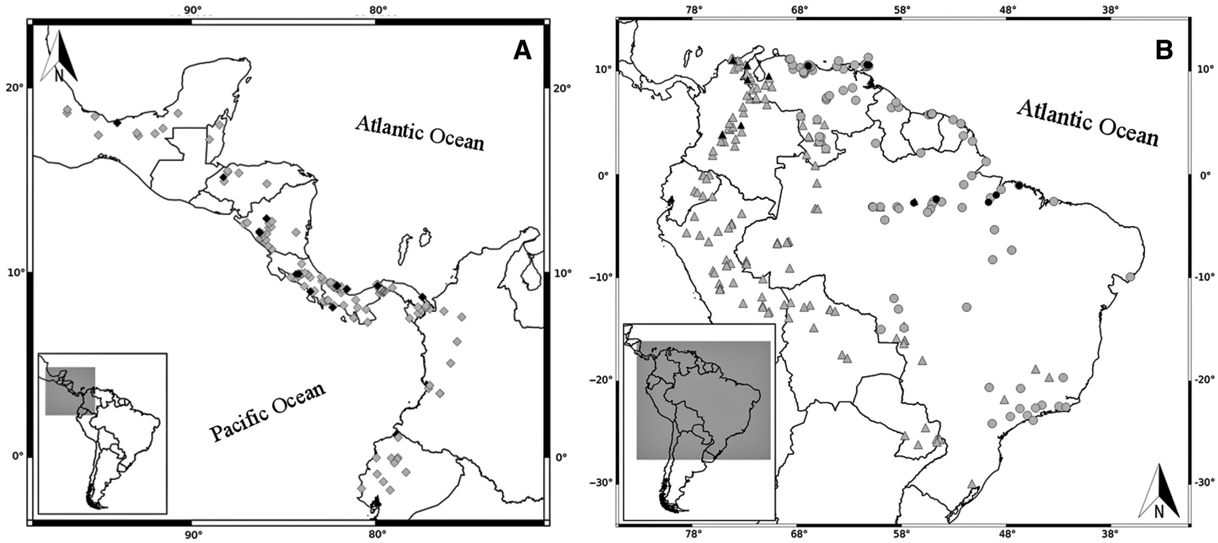

Figure 1: *Caluromys lanatus* and *Caluromys philander* are distributed exclusively in South America East of the Andes, while *Caluromys derbianus* is distributed West of the Andes and extending into Central America to about 20°N.
Distribution of studied specimens (in gray) including those with anomalies (in black) for (A) *Caluromys derbianus* (diamonds), (B) *Caluromys lanatus* (triangles) and *Caluromys philander* (circles).

Martin 2008, Valladares-Gómez et al. 2017, but see D'Elía et al. 2016).

Although dental anomalies have been described for species of Paucituberculata and Microbiotheria, only a few studies have documented them in didelphids (Chemisquy and Martin 2016, and references cited therein). Recent examination of several hundred crania of the genus *Caluromys* housed at different collections have presented us with the opportunity to describe dental anomalies in these New World marsupials. The genus *Caluromys* Allen, 1900 includes three species of arboreal marsupials with omnivorous or frugivirous-animalivorous diets (Santori et al. 2012, Astúa 2015). The different species are distributed from Central America *Caluromys derbianus* (Waterhouse, 1841) to northeastern Argentina *Caluromys lanatus* (Olfers, 1818) (Figure 1A and B), living in both primary and secondary forests from sea level to 2500 m.a.s.l. (Gardner 2007, Astúa 2015). Dental anomalies in *Caluromys* have been rarely documented; Astúa de Moraes et al. (2001) reported a specimen of *Caluromys philander* (Linnaeus, 1758) with a supernumerary tooth, while Miles and Grigson (1990) described the lack of both M4 in a specimen of the same species.

The main objectives of this contribution were the description and categorization of dental anomalies in the genus *Caluromys*, and their placement within a functional/non-functional context. Comparisons with other marsupials gave us the opportunity to provide a comprehensive analysis of anomalies, while discussing aspects related to species distribution and phylogeny.

Materials and methods

We studied 462 crania from the three recognized species in the genus *Caluromys*: *Caluromys derbianus* (n = 209), *Caluromys lanatus* (n = 95) and *Caluromys philander* (n = 158) (see Appendix 1 for a list of studied specimens). Only adult specimens (i.e. those with fully erupted molars in their final position) were used in our analyses.

Dental anomalies were recorded and classified according to four categories, as described by Martin (2007) and Chemisquy and Martin (2016): (1) Variations in occlusal and root morphology, referring to anomalies in teeth of the normal series (not of supernumerary teeth; e.g. missing protocones, double cusped premolars, molariform or simplified crowns, fused teeth); (2) Teeth in unusual positions (e.g. a flipped molar, a transversely oriented premolar); (3) Supernumerary or missing teeth in any position (loss not produced by a physical disturbance; considered as such when damage to bone is evident through a bony callus or remodeling in the mandible or maxilla of the studied specimens); and (4) The presence of unshed deciduous premolars (marsupials only shed a single post-canine tooth throughout their ontogeny, which is one of the first teeth to erupt; Luckett 1993).

Dental nomenclature follows Goin (2003). Tooth homologies follow Ungar (2010), in which the only deciduous tooth is the third upper/lower premolar (dP3/dp3), and the other teeth are abbreviated as follows: I/i, upper and lower incisors; C/c, upper and lower canine; P1/p1, P2/p2, P3/p3, upper and lower first, second and third premolars; M1/m1 to M4/m4, first to fourth upper and lower molars.

Table 1: Dental anomalies by type and sex in species of *Caluromys derbianus*, *Caluromys lanatus* and *Caluromys philander*.

Category	***C. derbianus*** **(n=209; 13♂, 8♀, 2 indet)**	***C. lanatus*** **(n=95; 4♂, 1♀, 2 indet)**	***C. philander*** **(n=158; 6♂, 4♀)**
Anomalies in M4/m4	12 (7♂, 3♀, 2 indet)	2 (1♂, 1♀)	–
Anomalies in premolars	3 (1♂, 2♀)	1 (1 indet)	2 (2♀)
Root anomalies	–	1 (1 indet)	1 (1♀)
Flipped crown	4 (1♂, 3♀)	–	1 (1♂)
Anomalies in position	–	1 (1♂)	–
Supernumerary teeth	2 (2♂)	–	–
Missing teeth	4 (4♂)	6 (4♂, 1♀, 1 indet)	6 (5♂, 1♀)
Unshed decidious teeth	2 (2♂)	1 (1♀)	–
Total anomalies	27	12	10

Between brackets, n is total number of studied specimens, followed by the number of specimens with anomalies per sex. Categories are described in the materials and methods section and follow Chemisquy and Martin (2016).

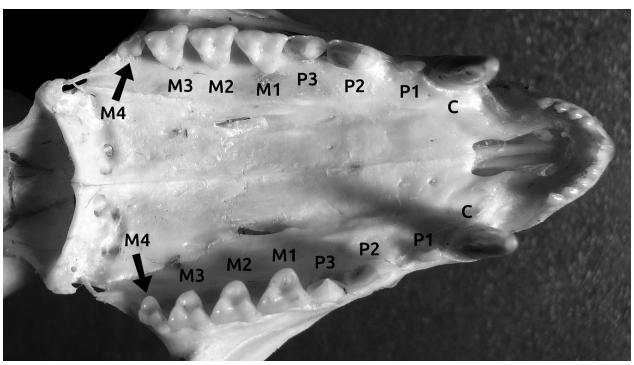

Figure 2: Abnormal crown morphology in right M4 of *Caluromys derbianus* (USNM 335006).

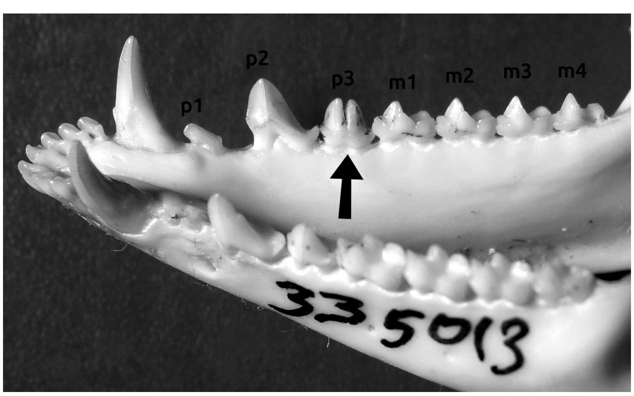

Figure 3: Abnormal crown morphology in right p3 of *Caluromys derbianus* (USNM 335013).

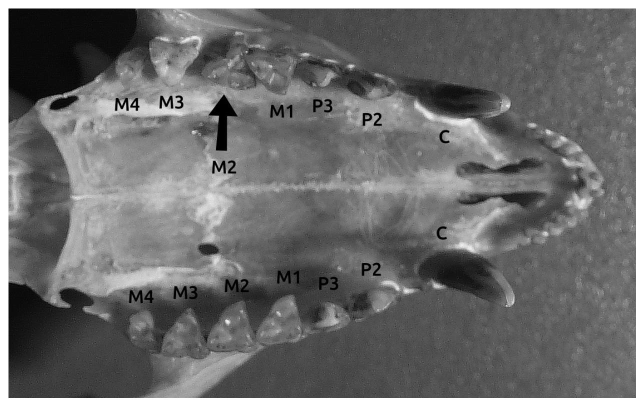

Figure 4: Specimen of *Caluromys derbianus* (USNM 578951) with flipped right M2.

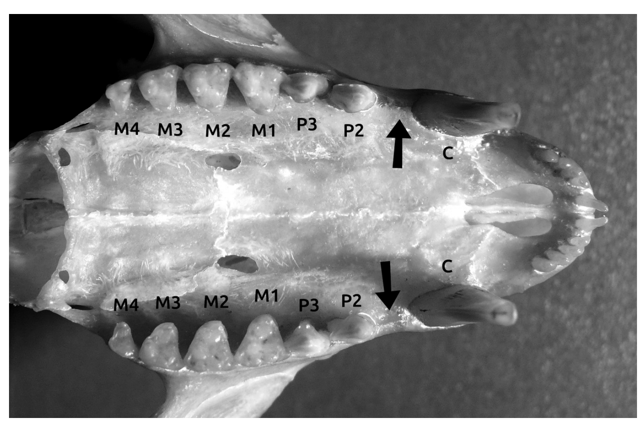

Figure 5: Specimen of *Caluromys derbianus* (USNM 271105) missing both P1.

Results

A total of 40 (8.7%) individuals with anomalies were found from the studied sample of 462 specimens (Appendix 1): 23 (11%) in *Caluromys derbianus*, seven (7.4%) in *Caluromys lanatus*, and 10 (6.3%) in *Caluromys philander* (Table 1). Due to some individuals presenting more than one anomaly, a total of 27 anomalies were found

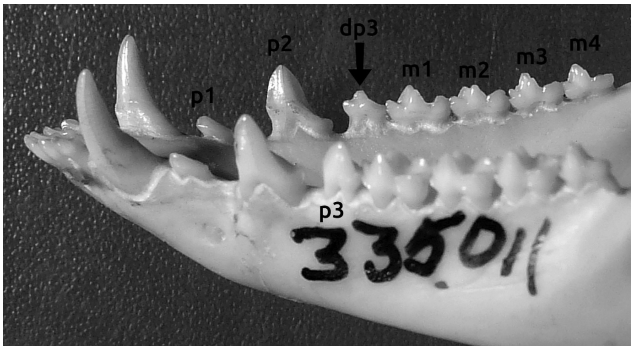

Figure 6: Presence of unshed deciduous right lower premolar (dp3) in *Caluromys derbianus* (USNM 335011).

in *C. derbianus*, 12 in *C. lanatus* and 10 in *C. philander* (Table 1).

Anomalies of all four categories were found in the three species, despite some differences in occurrence and anomaly type, with the exception of category 4 (unshed deciduous teeth) not found in *Caluromys philander* (Table 1). Only in a few number of specimens anomalies were bilaterally present (e.g. *Caluromys derbianus* AMNH 131708 with right and left m2 separated from m3 by a small diastema; *Caluromys lanatus* USNM 418464 with a missing right M4 and an anomalous crown morphology in the left M4), with most individuals presenting anomalies located in individual quadrants. In only a single specimen (*C. lanatus* USNM 371280) anomalies were on the same side but in the upper and lower dentition (i.e. missing right M4/m4).

The most common anomaly in *Caluromys derbianus* was represented by variations in the occlusal morphology of M4/m4 (n = 12) and premolars (n = 3). Anomalies in M4 showed undeveloped protocones (Figure 2) or reduced m4 crowns, while premolars showed double cusped (Figure 3) or molariform crowns. Other less common anomalies included twisted M2s on both maxillae, with the anterior region closer to the posterior of M1 (Figure 4), supernumerary teeth at the end of the upper toothrow (as m5), and missing teeth in some quadrants [e.g. left P1 in AMNH 139783 (Figure 5), left p3 in NMNH 297451] (Table 1). The most common anomaly in *Caluromys lanatus* and *Caluromys philander* were missing teeth

Table 2: Frequency of anomalies in marsupial species recorded to date.

Species	Total	Number of specimens with anomalies	%	Number of specimens without anomalies	%
Caluromys derbianus (Waterhouse, 1841)	209	23 (13 ♂, 8 ♀, 2 indet)	11	186	89
Caluromys lanatus (Olfers, 1818)	95	8 (4 ♂, 1 ♀, 3 indet)	8.4	87	91.6
Caluromys philander (Linnaeus, 1758)	158	10 (6 ♂, 4 ♀)	6.3	148	93.7
Caluromys philander[1]	82	1	1.2	81	98.8
Chironectes minimus[1] (Zimmermann, 1780)	141	1	0.7	140	99.3
Didelphis albiventris[2] Lund, 1840	393	32 (♂, ♀, indet)	8.1	361	91.9
Didlephis aurita[2] Wied-Newied, 1826	96	2 (♂, ♀, indet)	2.1	94	97.9
Didelphis marsupialis[2] Linnaeus, 1758	74	3 (♂, ♀, indet)	4.6	71	98.9
Didelphis albiventris[1]	655	3	0.5	652	99.5
Didlephis aurita[1]	337	1	0.3	336	99.7
Didelphis marsupialis[1]	872	9	1	863	99
Philander andersoni[1] (Osgood, 1913)	36	1 (♀)	2.8	35	97.2
Philander frenatus (Olfers, 1818)	244	2 (2 ♂)	0.8	242	99.2
Philander opossum[1] (Linnaeus, 1758)	767	2 (1 ♂, 1 indet)	0.3	765	99.7
Thylamys venustus[3,4] (Thomas, 1902)	253	0	0	253	100
Thylamys pallidior[3] (Thomas, 1902)	110	0	0	110	100
Lestodelphys halli[3] (Thomas, 1921)	300	0	0	300	100
Caenolestes fuliginosus[3] (Tomes, 1863)	40	6 (4 ♂, 2 ♀)	15	34	85
Lestoros inca[5] (Thomas, 1917)	70	21 (8 ♂, 12 ♀, 1 indet)	30	49	70
Rhyncholestes raphanurus[6] Osgood, 1924	53	10 (5 ♂, 5 ♀)	18.9	43	81.1
Dromiciops gliroides[6] Thomas, 1894	91	8 (7 ♂, 1 ♀)	8.8	83	91.2
Sminthopsis murina[7] (Waterhouse, 1838)	140	2	1.4	138	98.6
Anthechinus flavipes[7] (Waterhouse, 1838)	41	5	12.2	36	87.8
Dasyurus geoffroii[7] Gould, 1841	45	2	4.4	43	95.6
Planigale maculata[7] (Gould, 1851)	43	2	4.7	41	95.3

Previous information was retrieved from different sources, as follows: [1]Astúa de Moraes et al. (2001); [2]Chemisquy and Martin (2016); [3]Martin (2007); [4]includes *T. cinderella* (Thomas, 1902) and *T. sponsorius* (Thomas, 1921); [5]Martin (2013); [6]new information based on a more extensive dataset; [7] Archer (1975).

Table 3: Occurrence of dental anomalies in Caluromyinae and other New World marsupial subfamilies/families.

Type of anomaly	Anomalies in M4/m4	Anomalies in premolars	Root anomalies	Flipped crown	Anomalies in position	Missing teeth	Supernumerary teeth	Unshed deciduous teeth	Total anomalies per Family
Caluormyinae	**15** (**60**; **30**)	6 (25; 12)	2 (33.3; 4)	5 (**71.4**; 10)	1 (12.5; 2)	**15** (38.5; **30**)	3 (8.1; 6)	3 (**75**; 6)	48
Didelphinae (Didelphini)	5 (20; 9.4)	8 (**33.3**; 15.1)	4 (**66.7**; 7.5)	2 (28.6; 3.8)	5 (**62.5**; 9.4)	2 (5.1; 3.8)	**26** (**70.3**; **49.1**)	1 (25; 1.9)	53
Caenolestidae	2 (8; 5.1)	8 (**33.3**; 20.5)	–	–	2 (25; 5.1)	**21** (**53.8**; **53.9**)	6 (16.2; 15.4)	–	39
Microbiotheriidae	**3** (12; **37.5**)	3 (8.4; 25)	–	–	–	1 (2.6; 12.5)	2 (5.4; 25)	–	8
Total anomalies per category	25	24	6	7	8	39	37	4	

For each category, number of anomalies and their percentage (in brackets) are presented, in relation to the total number of anomalies in each category (column) and subfamily/family (row). Numbers in bold indicate the highest number of anomaly type per type in column, and subfamily/family per row, respectively.

(n = 6 and n = 5, respectively). Also, both species presented anomalies in the occlusal morphology as in *C. derbianus* (e.g. M4 without developed protocone, bicusped p2, and single-rooted P1/p1) (Table 1).

We also found adult individuals of both *Caluromys derbianus* and *Caluromys lanatus* with upper and lower deciduous premolars (Figure 6). These deciduous teeth were found in specimens with completely developed skulls, fully erupted teeth and signs of tooth wear, which in some cases showed worn cusps, indicating that individuals were fully-developed/grown adults. Males of *C. derbianus* showed a higher frequency of anomalies than females, with supernumerary, missing, and unshed deciduous teeth, as the most common anomalies (Table 1). In *C. lanatus* and *Caluromys philander*, no clear differences were found between males and females. Missing teeth were the most common anomaly in males of *C. lanatus* and *C. philander*, while females of *C. philander* had anomalies in premolars.

Comparisons with reports of anomalies in other marsupials are presented in Table 2. Caluromyines show a higher percentage than other didelphids, with values from 6.3 to 11% of the total analyzed specimens, and an average of 9.5%.

Dental anomalies in New World marsupials and their occurrence and type, discriminated by Subfamily/Family, are presented in Table 3. Comparing dental anomalies in Caluromyines to other Subfamilies of Didelphidae, the former show a higher frequency of anomalies in M4/m4 and missing teeth, and a few specimens with flipped crowns. When discriminated by category, New World marsupials produce more supernumerary or have missing teeth (Category 3, 76 anomalies), followed by anomalous crown morphologies (Category 1, 55 anomalies). Flipped crowns and anomalies in position (Category 2, 15 anomalies) are less common, and so is the presence of unshed deciduous teeth.

Discussion

The percentage of anomalies we found in caluromyines is higher than those previously described, in which a single supernumerary tooth (Astúa de Moraes et al. 2001) or missing M4 were found (Miles and Grigson 1990). This difference is probably due to a higher number of analyzed specimens in this work (e.g. 462 specimens vs. 82 by Astúa de Moraes et al. 2001), and a different conceptual framework in which we looked at anomalies (i.e. instead of focusing only in supernumerary teeth, we took a broader approach categorizing each type of anomaly). This difference also shows that, because dental anomalies influence the survival of individuals who possess them, larger samples are necessary in order to find anomalous specimens.

In our studied sample, we found more anomalies in *Caluromys derbianus* than in the other two species, with *Caluromys lanatus* showing an intermediate number (11–6.3%, as shown in Table 2). Although the three species have anomalies in all categories, *C. derbianus* has more anomalous M4/m4, and specimens with flipped crowns, while the other two species have a higher number of missing teeth. Of these, only the occurrence of flipped crowns might have severe consequences in mastication, as they involve the second molar in the upper dentition. The other anomalies seem to be less important from a functional perspective, especially when they occur at the end of the toothrow as missing or malformed M4/m4. Some of these types of anomalies (e.g. missing teeth, anomalous crowns) have also been documented in living species of Paucituberculata, but the main difference is that most missing teeth in paucituberculatans are lower incisiform teeth, located between the procumbent incisor and the second lower premolar (Martin 2007, 2013). As has been discussed elsewhere (Martin 2007, 2013, Chemisquy and Martin 2016), these teeth seem to have no function during occlusion and/or mastication. Contrary to this, didelphid species of the subfamily Didelphini have more anomalies as supernumerary teeth (49.1% of the total found in the group). *Dromiciops gliroides* shows a combination of supernumerary or missing teeth, and anomalous crowns mostly in premolars (Martin 2007).

When compared to other marsupial species, the percentage of anomalies in *Caluromys* spp. is similar to those found in *Dromiciops gliroides* Thomas, 1894 (8.8%) and *Didelphis albiventris* Lund, 1840 (8.14%), but are considerably less than those found in caenolestids (12.5%–30%; Martin 2007, 2013, Chemisquy and Martin 2016). On the contrary, they exceed those found in other didelphids (i.e. 0–3%; González 2000, Astúa de Moraes et al. 2001, Martin 2007, Chemisquy and Martin 2016).

Almost half of the anomalies found in *Caluromys derbianus* come from specimens living on islands, and a third of those from *Caluromys philander* show the same pattern (they are from Trinidad). Caluromyines are highly arboreal marsupials, have small litter sizes and longer life-spans, for which they can be considered *K* strategists in relation to other New World marsupials (Gentile et al. 2012). These conditions make them susceptible to local habitat modifications in the short term, which leads to isolation of local populations, although they seem to tolerate different levels of fragmentation and disturbance (Astúa 2015).

Dental anomalies in New World marsupials probably occur by the interaction of different processes, which could include inbreeding and limited gene flow, and environmentally related disturbances (Martin 2007, 2013, Chemisquy and Martin 2016). Based on the concept of morphogenetic fields, Miles and Grigson (1990) propose that supernumerary teeth are produced by an abnormally strong capacity of tooth formation (i.e. the dental lamina), which could explain why extra teeth usually occur at the end of the toothrow (as M5/m5). Other proposed ideas imply that supernumerary teeth arise from the splitting or dichotomy of a tooth primordium (Bateson 1894, Wolsan 1984). Recent works (e.g. Prochazka et al. 2010, Jernvall and Thesleff 2012) have consistently shown that tooth development is genetically controlled; the presence of extra teeth at the end of the toothrow can therefore be seen as a product of ill-controlled genetic signals, in which the lamina continues to produce teeth (see Harris 2009, Peterkova et al. 2014, and references cited therein). Following these concepts, missing teeth should occur due to a reduced capacity of the dental lamina to produce them, or an early termination of tooth "production" due to inhibition. These processes were described for rodents by Kavanagh et al. (2007), functioning as a quantitative inhibitory cascade model in which molar development depends on a balance between mesenchymal activators promoting knot induction, and inhibition expressed in previously initiated molars. Our compared data (Table 3) shows that supernumerary and missing teeth are the most common abnormalities observed in New World marsupials.

As for changes or abnormalities in crown morphology (e.g. double-cusped premolars, abnormal M4/m4), these have to occur in what has been described by Jernvall and Thesleff (2012) as the bell stage, during which species-specific cusp patterns emerge. At this stage, the crown of mammal teeth is formed by a set of secondary enamel knots giving rise to multicusped teeth, which can suffer gene mutations alternating cusp patterns (Jernvall and Thesleff 2012). Our data for *Caluromys* spp. and other New World marsupials shows that these abnormalities are found in teeth without occluding antagonists (e.g. premolars and M4/m4), and that no genetic or functional mechanisms are selecting against them (see Table 3).

From a functional point of view, the anomalies we found in *Caluromys* occur in areas of the toothrow with a low impact on the masticatory cycles, similar to what has been described in *Didelphis* spp. (Chemisquy and Martin 2016). Also, a higher consumption of fruit in the diet of caluromyines (Cáceres 2005, Casella and Cáceres

2006) is probably less susceptible to malocclusion than that of other didelphids, in which anomalies might have a stronger effect since they consume a larger proportion of harder items.

Depending on the position in which they occur, dental anomalies might have consequences in individuals' performance or survival. In some cases, anomalies might render individuals nonviable or simply unfit, reducing their lifespan (e.g. specimens with a rotated M2 crown). Other anomalies will have no effect on the individuals' fitness and will persist in the population (e.g. presence of supernumerary teeth at the end of the toothrow, unshed deciduous premolars, teeth with anomalous number of roots). Most of the anomalies described herein (except for rotated crowns) do not interfere with normal occlusion, apparently resulting in individuals which attain adulthood without functional problems.

As with all previously studied cases, dental anomalies in *Caluromys* spp. probably occur as a combination of multiple developmental, population-related and environmental factors. Unfortunately, data available for these species is fragmentary, therefore the causes of malformations with the information at hand could only be speculative, and are also beyond the scope of our work. Despite this, our findings provide a better understanding on the dental anomalies found in *Caluromys*, a genus of marsupial characterized by a somewhat different diet and spatial use than other New World counterparts. Our data reinforces the idea that dental anomalies can be predominantly found in areas of the toothrow where occlusion is not influenced by interlocking mechanisms during mastication, and are probably not directly related to diet or substrate use.

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Appendix 1: Analyzed specimens of *Caluromys* spp. and those with anomalies (in bold).

Caluromys derbianus: **Colombia**: AMNH 14189, AMNH 15074, USNM 334676 – 334678, USNM 4745. **Costa Rica**: AMNH **131706** – (**131708**) – 131712, AMNH 131733 – 131735, AMNH 135267, AMNH **135328** – **135329**, AMNH 135583, AMNH 137286 – 137287, AMNH 139278, AMNH 139281, AMNH **139678** – 139679, AMNH 139781, AMNH **139783**, AMNH 19202, AMNH 10057 – 10058, NMW 23347 – 23360, NMW 4231, USNM 12886, USNM 250280, USNM 284463 – USNM 284464, USNM A 22020. **Ecuador**: AMNH 47194, AMNH 63525 – 63526. **Honduras**: AMNH **126134**, AMNH 126980, USNM 148749, USNM 19462. **Mexico**: AMNH 185756, USNM 251470, USNM 251470, USNM **271105** – 271106. **Nicaragua**: AMNH 176710 – (**176711**) – AMNH 176714, AMNH 28331, AMNH **41395** – 41397, USNM **297451** – 297453, USNM 337504, USNM 339889 – 339894. **Panamá**: AMNH 164491, AMNH 18908 – **18913**, AMNH 266976, USNM 171033, USNM 179923, USNM 200289, USNM 243413, USNM 248351, USNM 257328, USNM 266873 – 266875, USNM 290878, USNM 291972, USNM 296188 – 296189, USNM 296344, USNM **297875** – 297877, USNM 298699, USNM 301131 – 301134, USNM 301547, USNM 302329, USNM 303233, USNM 304694, USNM 305145, USNM 306379, USNM 309256 – 309262, USNM 314551, USNM 315009 – 315013, USNM 322943 – 322945, USNM 331068, USNM 335001 – **335006**, USNM 335008 – (**335010**, **335011**, **335013**, **335024**) – 335027, USNM 337951 – 337953, USNM 360134 – 360138, USNM 362315 – 362317, USNM 396414, USNM 449559 – 449560, USNM 449562 – 449563, USNM 456809, USNM 464247, USNM 464517, USNM 503420, USNM 575393, USNM 578116, USNM 578118 – 578119, USNM 578934 – 578936, USNM 578938 – (**578940, 578941**) – **578951**, USNM **578953** – 578957. **Unkonwn localities**: USNM 253050, USNM 364951, USNM 398849.

Caluromys lanatus: **Argentina**: MACN 20450, MACN 21377 – 21378, MACN 23632, MACN 24272. **Bolivia**: AMNH 133205, AMNH 215001, MACN 50.181, MACN 50.188. **Brazil**: AMNH 133184, AMNH 133199 – 133200, AMNH 133204, AMNH 133206, AMNH 133208, AMNH 136161, AMNH 143016, AMNH 92760, AMNH 92882 – (**92883**) – 92884, AMNH 93530, AMNH 93967, NMW B 2596, USNM 546177. **Colombia**: AMNH 61580, AMNH 61582, USNM 541855 – 541856, AMNH 143522, AMNH **62241**, AMNH 75886, AMNH 76767 – (**76768**) –76770, USNM 251901 – 251902, USNM **271317**, USNM 280900 – 280904, USNM 280906 – **280908**, USNM 544393 – 544395. **Ecuador**: AMNH 182938, AMNH 68281 – 68282, NMW 12098, NMW 26279, USNM 528318 – 528319. **Paraguay**: AMNH 66780. **Perú**: AMNH 230001 – 230002, AMNH 273038, AMNH 273059, AMNH 75911 – 75913, AMNH 78951, AMNH 98657, AMNH 98659 – 98661, AMNH 71977 – 71984, MUSM 15290 – 15291, USNM 149001, USNM 194375, USNM 364159 – 364160, NMW 1791/B 2587 – 1792/B 2586. **Venezuela**: AMNH 24327, AMNH 78101, USNM **371280**, USNM 388327, USNM 388330 – 388334, USNM 406874 – 406875, USNM 406878 – 406879, USNM 416932, USNM **418464**, USNM 560679.

Caluromys philander: **Brazil**. AMNH 139815 – 139816, AMNH 203350 – 203352, AMNH 2263, AMNH **93529**, AMNH 93531, AMNH 94894 – (**94896**) – 94899, AMNH 95524 – 95537, AMNH **95761**, AMNH 95972, AMNH 95974 – 95975, AMNH 96641 – (**96648**) – 96652, MACN 24278, MACN 50.30, NMW 24043, NMW 28622 – 28624, NMW B 2588, NMW B 2590 – 2592, NMW B 2597 – 2600, NMW B 2603, USNM 393443 – (**393452**) – 393456, USNM 461364, USNM 545388 – 545391. **French Guiana**: AMNH 266408 – 266409, AMNH 267001 –

Appendix 1 (continued)

267002, AMNH 267330, AMNH 267332 – 267335, AMNH 267337. **Trinidad and Tobago**: AMNH **169670**, AMNH 169740, AMNH 169762, AMNH 171380, AMNH 173985, AMNH 173999, AMNH 174001 – (**174002**, **174003**) – 174006, AMNH 174009 – 174010, AMNH 174161, AMNH 174234, AMNH 186436, AMNH 208993 – 208995, AMNH 234979 – 234980, AMNH 234986, AMNH 234988 – 234989, AMNH 235006, AMNH 29687, AMNH 5943 – 5951, AMNH 5953, AMNH 169668, AMNH 4766, USNM 124648, USNM 85557. **Venezuela**: AMNH 16133, AMNH 16955, AMNH 76969, AMNH 31533, USNM 143796 – 314170, USNM 314992 – 314993, USNM **370001**. **North Carolina Zoo**. AMNH 96623 – 96634, AMNH 96636 – 96640. **Unknown locality**: NMW B 2595.

AMNH: American Museum of Natural History, New York (USA); MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (Argentina); USNM: United States National Museum – Smithsonian Institution, Washington DC (USA); MUSM: Museo de la Universidad de San Marcos, Lima (Perú); NMW: Naturhistorisches Museum Wien, Vienna (Austria).
Unknown Zoo: AMNH 48188.

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