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UNEXPECTED INHIBITORY CASCADE IN THE MOLARIFORMS OF SLOTHS (FOLIVORA, XENARTHRA): A CASE STUDY IN XENARTHRANS HONOURING GERHARD STORCH'S OPEN-MINDEDNESS

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Abstract: The inhibitory cascade (IC) represents a developmental model that explains the evolution of molar relative sizes, originally described in rodents but later validated in several mammalian groups. The IC comprises signalling molecules produced by the first molar buds that inhibit the development of subsequent molars and molecules from surrounding tissues that have opposite effects. Sloths, as xenarthrans, present many peculiarities in their dentition, like tooth and enamel loss, homodonty, and changes in the typically mammalian dental formula. Here, we test the existence of an IC and explore the evolution of the lower dentition in sloths. We studied the variability of molariform proportions in 20 specimens of the Late Pleistocene ground sloth *Lestodon armatus*. We also analysed molariforms proportions in 53 sloth genera to explore evolutionary trends. Our results show that the lower dentition of most sloths complies with the IC model, despite the difficulties of assessing dental homologies with other mammals. Furthermore, we tested the existence of different patterns among families, obtaining support for models taking mylodontids and orophodontids separately from the rest of sloths. Also, members of Mylodontidae show a unique IC pattern, with a slope considerably higher than 2 and an mf1 ≤ mf2 << mf3 configuration. This pattern could be related to the morphological adaptations to grazing showed by mylodontids during most of their evolutionary history.

Key words: sloths, inhibitory cascade, macroevolution, tooth evolution, molariforms

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Introduction

One of us (RAF) had the pleasure to meet Gerhard Storch in connection with the preparation of the proceedings of the Xenarthra meeting held in Jena in 2001, published as a special issue of Senckenbergiana biologica (Fariña et al. 2003). Here we intend to honour his wide legacy that dealt with taxonomy, palaeobiology, biochronology, and palaeobiogeography of mainly small mammals in which he made relevant contributions (Franzen et al. 2018). Among the several Palaeogene taxa Storch described, an astonishing finding of a complete skeleton of a clearly ant-eating mammal in Eocene sediments from a pit not far from the city of Frankfurt am Main, led Storch (1981) to create the genus *Eurotamandua*. Originally, as the name implies, considered as the first myrmecophagid (Xenarthra) outside of South America, it was later classified as a basal member of Afrotheria (see Hunter and Janis 2006), and finally as a pholidotan without scales (Gaudin et al. 2009).

Xenarthrans are a group of mammals that include small to medium size armadillos, anteaters, and tree sloths as living species. However, their diversity in the fossil record is astonishing, including many glyptodonts and ground sloths (some of gigantic size; see Fariña et al. 1998, Christiansen and Fariña 2003) as completely extinct forms. Xenarthrans originated in South America during the early Cenozoic and, following a long-term diversification in that subcontinent, they spread into Central and North America following the Great American Biotic Interchange (Fariña et al. 2013). Prior to the extinctions near the Pleistocene-Holocene limit, the group reached great taxonomic and morphological diversity (Varela et al. 2018). Folivora (see Fariña and Vizcaíno 2003), the group that includes both living and extinct sloths, is currently represented by only two genera, the obligatory

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arboreal sloths *Bradypus* and *Choloepus*. However, as mentioned before, the fossil history of this clade was much more diverse along the Cenozoic, including about 90 genera (McKenna and Bell 1997), a number continuously growing with new findings in less-explored parts of the Americas (e.g., Pujos et al. 2012).

Xenarthrans differ from the rest of the mammalian clades by the individual morphology and number of teeth (McDonald 2003). When present, teeth in most adult xenarthrans lack enamel and are usually homodont, hypselodont, tubular, and primarily composed of orthodentine and vasodentine, which makes it difficult to identify homologies with the teeth and cusps of other mammals (Vizcaíno 2009, Hautier et al. 2016). In sloths, the dentition is reduced to a maximum of five upper and four lower teeth, with caniniforms (cf) present in megalonychids and some nothrotheriids, megatheriids, and mylodontids (Vizcaíno 2009). Hautier et al. (2016) studied the prenatal dental ontogeny of extant sloths, showing that the upper caniniforms are not homologous in both genera and their lower caniniforms are not homologous to the lower canines of other mammals. Furthermore, based on the timing of mineralizations of each tooth, they showed that the lower molariforms (mf) of both sloths are probably homologous to the dp3, dp4, and m1 of the rest of mammals. These results depict the complex evolution of the dentition in these two distantly related sloths (Gaudin 2004, Varela et al. 2018, Delsuc et al. 2019, Presslee et al. 2019) as well as in Folivora in general, which highlights the difficulties of defining dental homologies in extant and extinct sloths.

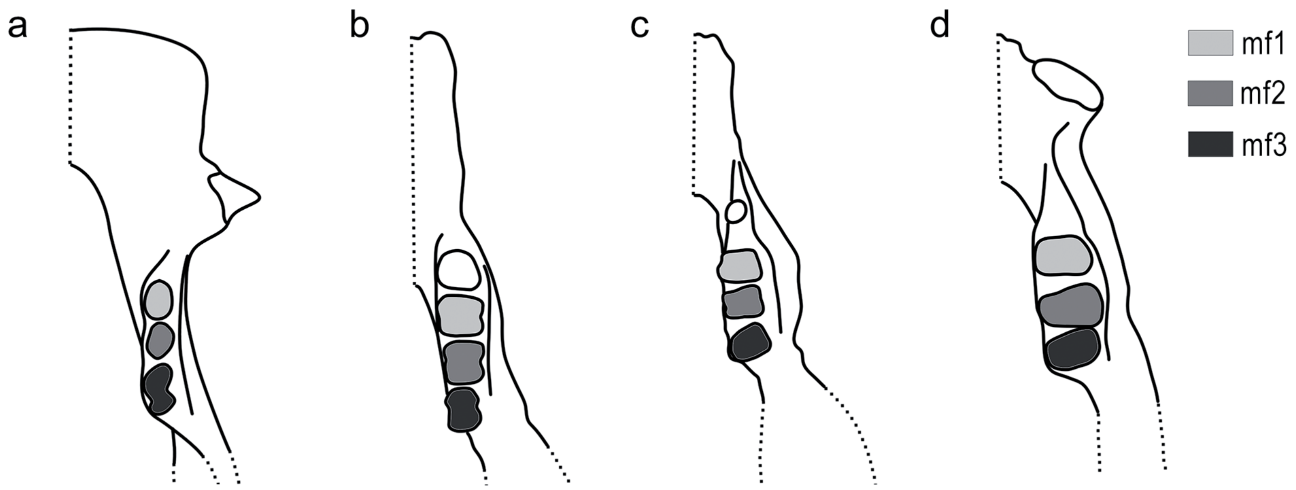
The evolutionary developmental (evo-devo) field consists of the integration of evolutionary, adaptational, and developmental approaches to explore the mechanistic relationships between the processes of individual development and phenotypic change during evolution (Müller 2007). The mammalian dentition represents a great system for the study of macroevolutionary patterns and the link between phenotypic variation, development, and evolutionary processes in deep time, allowing the inclusion of fossil taxa many times largely known by their tooth remains. Some years ago, Kavanagh et al. (2007) established a developmental model that can explain the evolution of the relative sizes of lower molars in murine rodents. The inhibitory cascade model (IC model) showed that signalling molecules produced by the developing first molar buds inhibited the development of subsequent molars, while molecules from the surrounding tissues had the opposite effect. Consequently, this balance between inhibition and activation during molar development results in a predictable relationship between molar sizes, with phenotypes (and their change across taxa and time) constrained to fall within expected patterns, namely m1 > m2 > m3, m1 ≈ m2 ≈ m3, or m1 < m2 < m3. The IC model has been studied in several extant (Kavanagh et al. 2007, Polly 2007, Labonne et al. 2012, Asahara 2013, Bernal et al. 2013) and extinct (Wilson et al. 2012, Schroer and Wood 2015, Asahara et al. 2016, Evans et al. 2016, Gomes Rodrigues et al. 2017) mammals, with evidence supporting its existence deep in mammalian evolution (Halliday and Goswami 2013). Although it applies to many clades, it cannot be generalized across all mammals, and some examples of mammalian groups that fall outside the model prediction also exist (Polly 2007). Moreover, different patterns in different mammalian groups were found, supporting the existence of different intensities in inhibition and activation across the cascade, and allowing the evolution of different morphotypes not strictly predicted by the model (Asahara 2013). Interestingly, in many reported cases, this variability associated with the inhibitory cascade is related to different adaptations to certain diets. For example, in murine rodents, faunivorous species show larger m1 (and loss of m3), whereas herbivorous species have approximately equal-sized molars (Kavanagh et al. 2007). In canids, carnivorous species exhibited the pattern m1 >> m2 >> m3, omnivorous species exhibited m1 > m2 > m3 and insectivorous species have equal-sized molars (Asahara 2013). Finally, Evans et al. (2016) reported that an inhibitory cascade pattern was present along the dp3, dp4, and m1 in hominins, integrating to the already proposed cascade through m1, m2, and m3 and supporting the existence of a developmental control across the five teeth (the idea of a consistent pattern across the primary dentition was originally proposed by Butler 1939, but the exact mechanism was unknown at the time).

In this study, considering the dental homologies of sloths (Hautier et al. 2016) and the existence of an inhibitory cascade in dp3, dp4, and m1 in hominins (Evans et al. 2016), we explore the evolution of the lower dentition in sloths aiming at testing the existence of the inhibitory cascade in their molariforms. We also discuss the significance of the observed patterns across sloth families and their potential relationship with diet adaptations.

Materials and methods

Taxon sampling and data acquisition

In order to study the existence of the inhibitory cascade in the lower dentition of sloths, we focused on the dental dimensions of the last three molariforms. These last teeth are commonly named mf1, mf2, and mf3 and are morphologically different from the first lower tooth, which has a caniniform morphology in most sloths and is referred as cf1. However, some sloths, like the Megatheriinae, present a first tooth with molariform morphology and thus have a lower dental formula composed of mf1, mf2, mf3, and mf4. In those cases, we considered the last three molariforms as homologous with the last three molariforms of the rest of sloths (as tentatively proposed by Hautier et al. 2016) and the first molariform as homologous with the caniniform, with mf2, mf3, and mf4 considered as mf1, mf2, and mf3 in those taxa (Text-fig. 1). We collected data from juvenile and adult specimens of *Lestodon armatus*, a fossil ground sloth belonging to the family Mylodontidae, deposited in the collections of Museo Nacional de Historia Natural, Montevideo, Uruguay (MNHN); Museo Municipal “Bautista Rebuffo”, Colonia, Uruguay (MMBR); Museo Paleontológico “Armando Calcaterra”, Colonia, Uruguay (MPAC); Colección Arroyo del Vizcaíno, Sauce, Uruguay (CAV); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina (MACN); Museo de La Plata, La Plata, Argentina (MLP), in order to explore the molariforms variability among a single species (Tab. 1). The



Text-fig. 1. Examples of lower dentition and molariforms homologies in the four families of extinct sloths. a: Mylodontidae, b: Megatheriidae, c: Nothrotheriidae, d: Megalonychidae.

largest mylodontid *Lestodon armatus* was selected because it is probably the most abundant ground sloth found in Pleistocene deposits of Uruguay (Fariña et al. 2014, Varela and Fariña 2016), along with the large number of remains found in Argentina and Brazil, and because, despite this, it remains relatively little studied. We also collected data from sloth genera covering all sloth families from a revision of the literature, as well as published images and measurements of museum specimens (Tab. 2) to evaluate the IC model in this clade. In this case, a single adult individual was measured, which (although not ideal, is common in macroevolutionary analyses covering fossil species due to the limited sample or fragmentary nature of many specimens) could produce some artefacts in the analysis and should be considered when discussing the results. A total of 20 specimens of *L. armatus* were included in the first analysis, while a total of 53 sloth genera were included in the second approach.

Table 1. Molariforms area measurements and proportions in studied specimens of *Lestodon armatus*. Measurements in mm^2. %mf2: percentage of area occupied by mf2 in relation to the total area occupied by the last three teeth.

Specimen	mf1	mf2	mf3	mf2/ mf1	mf3/ mf1	%mf2
CAV 125	543.0	563.2	720.0	1.04	1.33	30.8
CAV 391	364.9	419.3	639.5	1.15	1.75	29.5
CAV 595	404.2	458.5	650.0	1.13	1.61	30.3
CAV 648	501.4	536.8	685.4	1.07	1.37	31.1
CAV 847	405.1	436.0	543.2	1.08	1.34	31.5
CAV 897	486.8	488.4	687.5	1.00	1.41	29.4
CAV 898	122.6	155.7	212.0	1.27	1.73	31.8
CAV 1261	381.2	401.1	499.9	1.05	1.31	31.3
CAV 1571	406.4	405.0	484.2	1.00	1.19	31.3
CAV 1572	327.7	344.5	438.5	1.05	1.34	31.0
MACN 9470	467.8	496.8	722.9	1.06	1.55	29.4
MACN 10830	471.6	582.7	867.7	1.24	1.84	30.3
MLP 3-29	529.4	619.1	806.8	1.17	1.52	31.7
MLP 3-30	342.4	385.8	607.5	1.13	1.77	28.9
MMBR 1110	68.5	68.5	92.9	1.00	1.36	29.8
MMBR sn-5	295.5	339.6	503.1	1.15	1.70	29.8
MNHN 2776	388.7	396.8	515.0	1.02	1.32	30.5
MNHN 2784	327.7	360.0	549.0	1.10	1.68	29.1
MNHN 2785	429.1	447.3	614.1	1.04	1.43	30.0
MNHN 2786	472.2	488.6	690.8	1.03	1.46	29.6

Tooth area is commonly measured by the product of the tooth length and width in most mammalian groups. However, in the case of sloths, especially mylodontids, the teeth are circular, elliptical, and/or lobated in section (Text-fig. 1). Therefore, we measured occlusal tooth area using ImageJ (Rueden and Eliceiri 2019) in images of the lower molariform row from published literature and collection specimens (Tabs 1, 2). A similar approach was previously used by Vizcaíno et al. (2006) in sloths for the study of the dental occlusal surface area and its relation with body mass and food habits.

The inhibitory cascade model

The IC model, originally proposed by Kavanagh et al. (2007), assumes a linear effect of the activator and inhibitor ratio on tooth proportions. Relative molar size and position follows the equation $y = 1 + [(a - i)/i](x - 1)$ where y is the relative molar size estimated from occlusal area, x is the position of the molar in the tooth row, a is the strength of activation, and i is the strength of inhibition. This equation predicts that M1 = 1, M2 = a/i and M3 = $2a/i - 1$.

The majority of the published research on the IC model used the RMA model in order to fit regressions. However, there is a current discussion regarding the use of OLS and RMA regressions and their impact on parameter estimations (Smith 2009). Considering this, and in order to compare our results with published analyses, we used both OLS and RMA to fit regressions to the *Lestodon* data. Furthermore, the lack of independency in biological data due to the existence of phylogenetic relationships between species has been

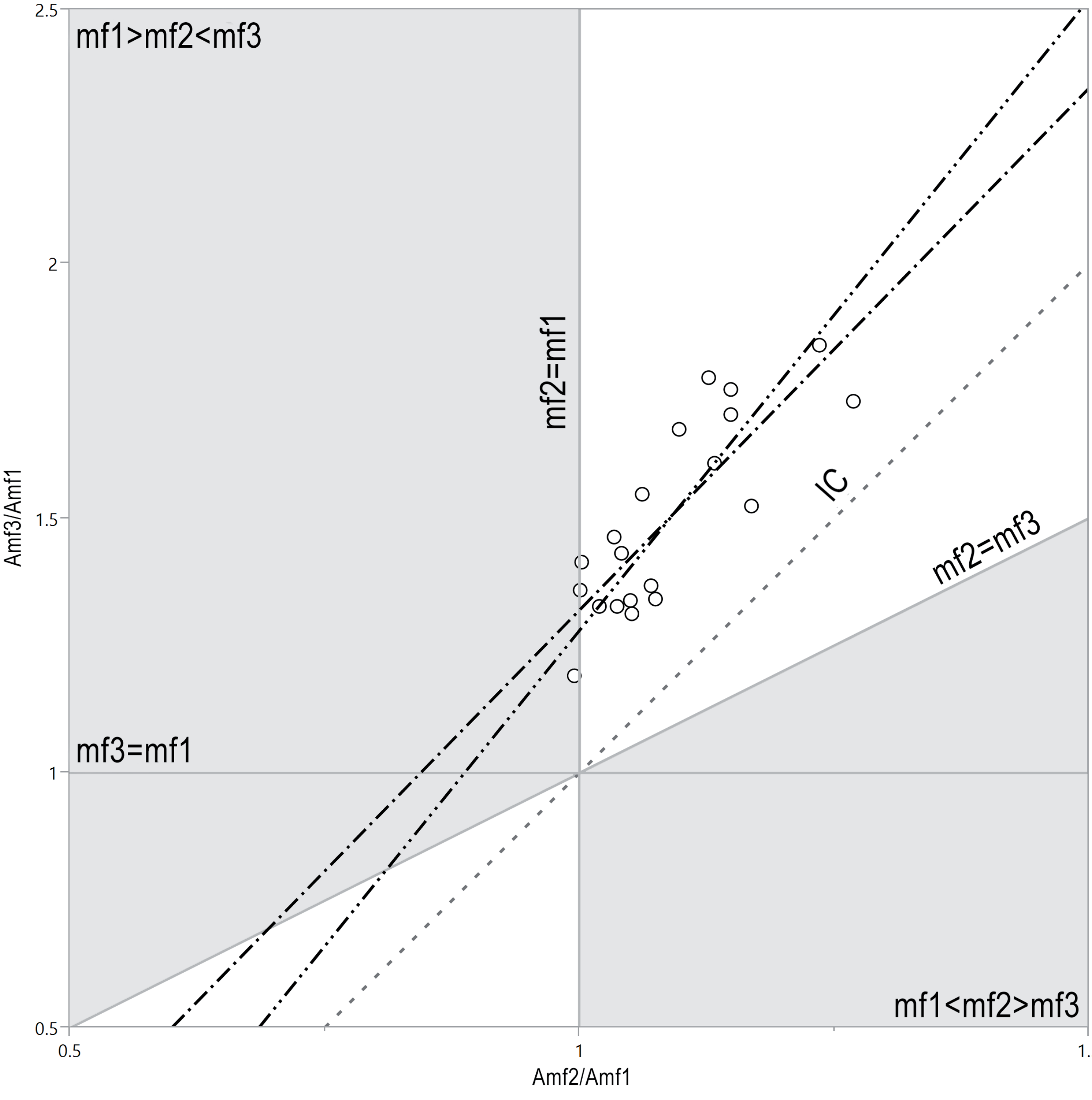
Table 2. Molariforms area measurements and proportions in studied sloth genera. Measurements in mm^2. cf: caniniform, mf: molariform, %mf2: percentage of area occupied by mf2 in relation to the total area occupied by the last three teeth.

Genus	cf1	mf1	mf2	mf3	mf2/mf1	mf3/mf1	%mf2	Reference
Octodontotherium	106.9	141.8	308.1	257.5	2.17	1.82	43.6	Hoffstetter 1954
Octomylodon	–	665.2	745.4	761.0	1.12	1.14	34.3	Scillato-Yané 1977
Pseudoprepotherium	215.8	191.4	210.8	349.2	1.10	1.82	28.1	Hirschfeld 1985
Thinobadistes	333.7	150.5	227.2	489.7	1.51	3.25	26.2	Webb 1989
Lestodon	505.5	394.6	427.1	587.4	1.09	1.50	30.3	This work
Pleurolestodon	453.0	328.0	340.4	660.5	1.04	2.01	25.6	Rovereto 1914, Saint-André et al. 2010
Glossotherium	374.6	424.2	567.7	1097.7	1.34	2.59	27.2	Mcafee 2009
Paramylodon	242.8	380.5	411.6	792.9	1.08	2.08	26.0	Mcafee 2009
Nematherium	35.5	44.8	51.6	79.0	1.15	1.76	29.4	Scott 1904
Catonyx	337.0	233.1	231.9	342.4	0.99	1.47	28.7	Cartelle et al. 2009
Scelidotherium	196.9	182.8	186.9	304.6	1.02	1.67	27.7	Bargo 2001a
Mylodon	222.7	316.2	354.3	462.8	1.12	1.46	31.3	Bargo 2001a
Acratocnus	61.2	50.0	56.3	59.7	1.13	1.20	33.9	Matthew and Paula Couto 1959
Neocnus	10.3	20.4	21.4	25.2	1.05	1.23	32.0	Matthew and Paula Couto 1959
Parocnus	24.8	57.5	69.3	89.3	1.21	1.55	32.1	Matthew and Paula Couto 1959
Megalocnus	150.3	291.2	342.9	404.0	1.18	1.39	33.0	Matthew and Paula Couto 1959
Pliometanastes	102.4	245.5	261.0	271.2	1.06	1.10	33.6	Hirschfeld 1981
Megalonyx	350.1	259.1	273.8	278.3	1.06	1.07	33.8	Savage 1946
Pronothrotherium	22.1	80.0	93.0	91.7	1.16	1.15	35.1	Rovereto 1914
Mionothropus	37.9	115.5	97.6	102.7	0.85	0.89	30.9	De Iuliis et al. 2011
Nothrotherium	–	84.8	95.2	98.0	1.12	1.16	34.2	Quiñones et al. 2017
Nothrotheriops	–	186.2	216.6	221.8	1.16	1.19	34.7	Quiñones et al. 2017
Eucholoeops	62.1	75.7	79.8	86.9	1.05	1.15	32.9	De Iuliis et al. 2014
Hapalops	33.7	48.8	54.6	60.5	1.12	1.24	33.3	Scott 1903
Eremotherium	2013.5	2686.3	2275.5	1770.8	0.85	0.66	33.8	McDonald and Lundelius 2009
Megatherium	1902.7	2396.8	2155.5	1442.2	0.90	0.60	36.0	Bargo 2001a
Schismotherium	20.8	36.4	46.4	54.3	1.27	1.49	33.8	Scott 1904
Pelecyodon	8.5	32.8	42.2	44.1	1.29	1.34	35.5	Scott 1904
Ahytherium	88.0	321.9	329.1	360.4	1.02	1.12	32.5	Cartelle et al. 2008
Proscelidodon	103.3	98.0	108.1	138.5	1.10	1.41	31.4	Taglioretti et al. 2014
Prepoplanops	47.2	119.9	123.9	146.0	1.03	1.22	31.8	Carlini et al. 2013
Anisodontherium	684.1	695.7	560.9	418.6	0.81	0.60	33.5	Brandoni et al. 2011
Urumacotherium	186.9	140.8	125.3	117.1	0.89	0.83	32.7	Negri and Ferigolo 2004
Simomylodon	138.6	99.0	106.0	193.5	1.07	1.95	26.6	Saint-André et al. 2010
Octodontobradys	223.1	271.6	349.3	330.9	1.29	1.22	36.7	Dos Santos et al. 1993
Brievabradys	42.8	19.7	21.2	28.7	1.07	1.46	30.4	Villarroel 2000
Lestobradys	310.0	231.3	268.5	448.4	1.16	1.94	28.3	Rinderknetcht et al. 2010
Valgipes	139.5	124.2	122.0	136.7	0.98	1.10	31.9	Cartelle et al. 2009
Bolivartherium	305.3	243.9	326.0	507.0	1.34	2.08	30.3	Carlini et al. 2006
Thalassocnus	–	146.9	161.7	183.7	1.10	1.25	32.9	Mcdonald and Muizon 2002, Muizon et al. 2003
Pyramiodontherium	1325.5	1678.4	1470.4	903.4	0.88	0.54	36.3	Carlini et al. 2002
Pseudortotherium	24.0	72.2	67.7	65.7	0.94	0.91	32.9	Scillato-Yané 1981
Xyophorus	15.1	56.5	63.9	62.1	1.13	1.10	35.0	Brandoni 2014
Megathericulus	276.1	333.2	346.5	351.1	1.04	1.05	33.6	Pujos et al. 2013
Diabolotherium	131.4	143.8	163.6	154.7	1.14	1.08	35.4	Pujos et al. 2007
Pseudoglyptodon	50.3	31.9	41.7	47.9	1.31	1.50	34.3	Engelmann 1987
Baraguatherium	–	252.7	285.8	222.9	1.13	0.88	37.5	Rincón et al. 2017
Aymaratherium	33.8	172.1	185.9	159.3	1.08	0.93	35.9	Pujos et al. 2016
Australonyx	152.1	283.8	302.4	305.8	1.07	1.08	33.9	De Iuliis et al. 2009
Lakukullus	34.7	129.8	153.8	172.8	1.19	1.33	33.7	Pujos et al. 2014
Prepotherium	25.6	65.5	66.1	69.7	1.01	1.06	32.8	Scott 1904
Bradypus	7.8	12.0	13.2	16.8	1.10	1.40	31.4	This work*
Choloepus	31.6	16.8	17.8	21.7	1.05	1.29	31.6	This work*

* Measurements taken from computerised tomography in digimorph.org.

recognized for a long time (Felsenstein 1985). In fact, some studies have used phylogenetic comparative methods to study the IC model in some groups (Bernal et al. 2013, Carter and Worthington 2016). In the present study, we employed PGLS to address the existence of the IC model in sloths. Specifically, we used the function corPagel from the package ape (Paradis and Schliep 2018) to define a correlation structure derived from Brownian motion allowing lambda to be estimated by the function. Also, we accounted for unequal tip variances due to a non-ultrametric tree. The OLS and RMA models were fitted using the software Past (Hammer et al. 2001), while the PGLS models were fitted using the package nlme (Pinheiro et al. 2012) for the software R (R core team 2019). In order to contemplate the phylogenetic relationships among the studied sloths, we used the phylogenetic framework previously used by Delsuc et al. (2019) for the study of the ancestral reconstruction of the dental configuration. For this, we used a backbone constraint based on Delsuc et al. (2019) molecular results on the morphological phylogeny proposed by Varela et al. (2018).

First, we evaluated the existence of the IC in all the data. However, we further tested the model after the exclusion of *Octodontotherium*, as this taxon was clearly an outlier when the data were plotted (see Text-fig. 4). The placement of this taxon could be explained by the unclear relationship of orophodontids with the rest of sloths and, therefore, the potential inexistence of homologies among their teeth. Alternatively, we tested the existence of an IC in the first three teeth of sloths, i.e., the first caniniform/molariform and the subsequent mf1 and mf2, to account for the existence of a different pattern as well as the potential influence of the first tooth on the last three teeth.



Text-fig. 2. Developmental morphospace of molariform ratios in *Lestodon armatus* compared to the IC model. Dash-dot line (-.-), show OLS line; dash double-dot line (-..-) shows RMA line.

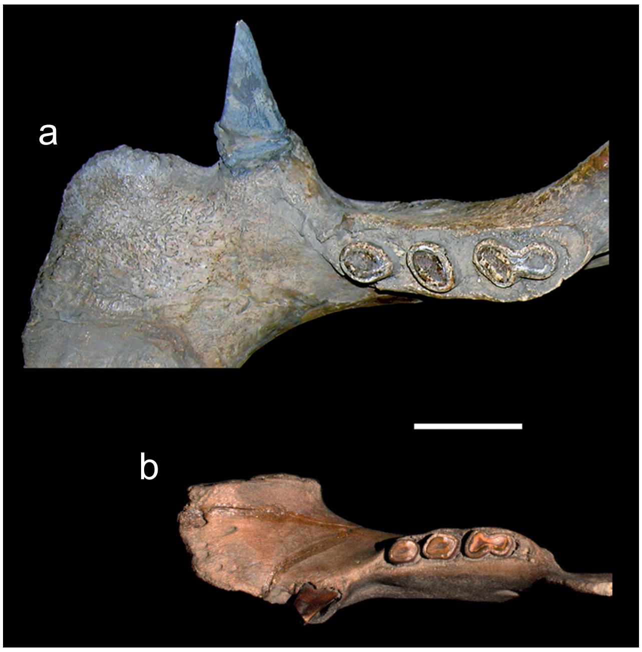
Furthermore, considering that the inhibitory cascade model predicts that the tooth placed in the middle should occupy 1/3 of the sum of the occlusal area, we calculated this value for each family and tested for significant differences with ANOVA and Tukey's multiple comparisons test ($p < 0.05$).

Finally, based on Tukey's test, we evaluated the possibility of different families showing different patterns regarding the existence and intensity of the IC model. For this, we included families as a categorical variable and compare different models using AIC.

Results

Lestodon armatus

A significant positive correlation ($r^2 = 0.66$, $p < 0.01$) was found between the ratios of mf2 and mf1, and mf3 and mf1 in *L. armatus*. Regarding the IC model predictions, the regression analysis showed a slope of 2.05 (CI: 1.13–2.54) for OLS and 2.48 (CI: 1.38–3.05) for RMA, and an intercept of −0.73 (CI: −1.26–0.22) for OLS and −1.20 (CI: −1.82–0.02) for RMA, consistent with the IC model (Text-fig. 2). However, the results indicate that, even if *L. armatus* comply with the IC model, some specimens almost fall outside the strict IC model prediction, with mf1 and mf3 larger than mf2. When observing the different specimens of *L. armatus* in detail, it is evident that the mf3 is always the largest tooth (even in juvenile specimens), while mf1 and mf2 show more variability and overlap in their size (Text-fig. 3). On the other hand, the mf2 occupied roughly 30% on average among the studied individuals, well below the prediction of the IC model. Alternatively, considering the great variability in the caniniform size in this taxon, a preliminary test (data not shown) exploring the existence of an IC among the first three teeth with a lower sample showed a significant correlation and a slope of 1, clearly inconsistent with the IC model.



Text-fig. 3. Mandibles of (a) adult (MACN 10830) and (b) juvenile (CAV 898) specimens of *Lestodon armatus*. Scale bar 5 cm.

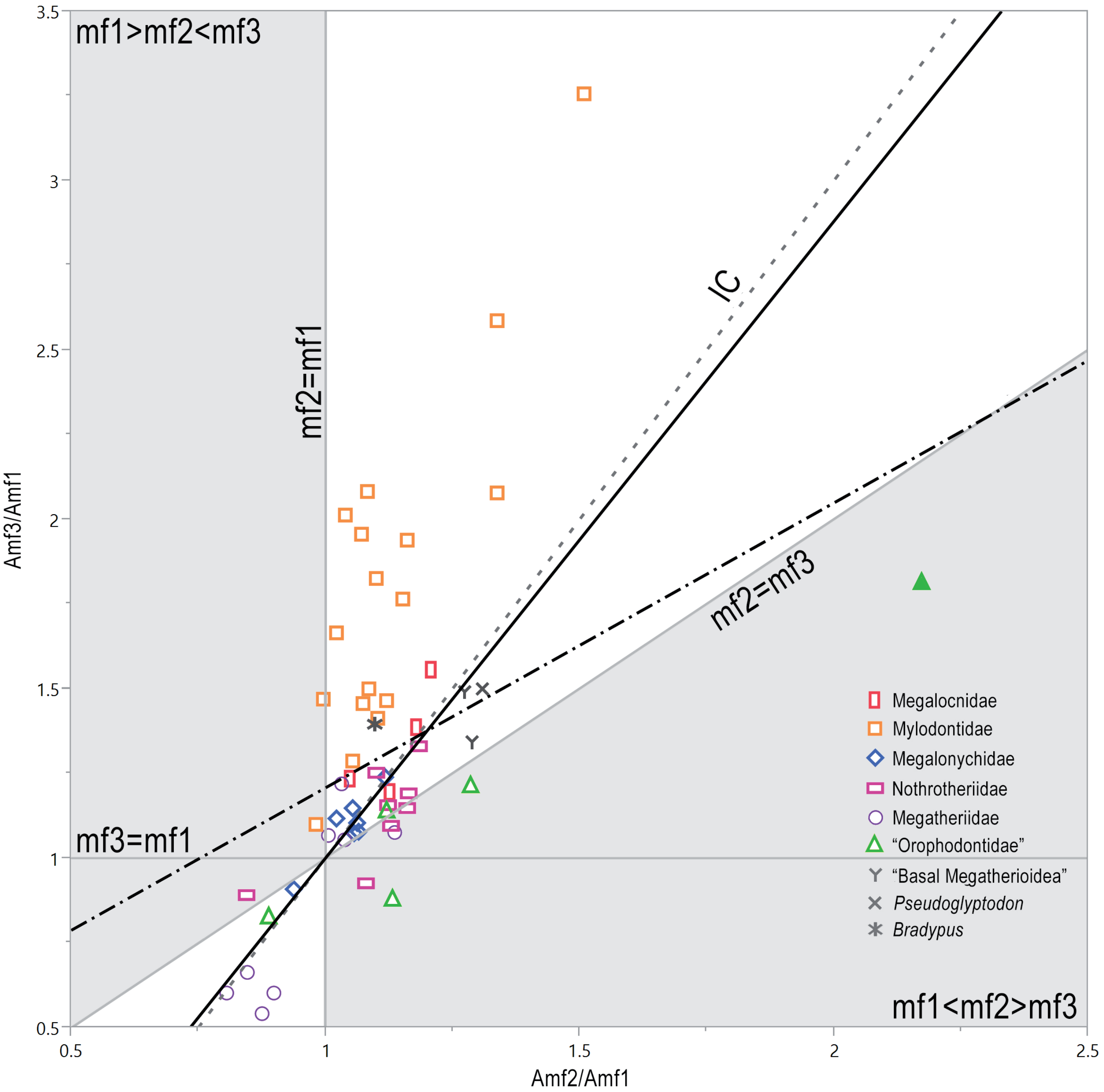
Sloths

Regarding the data set that includes taxa from all the families of sloths, a significant correlation was found between the ratios (Slope: 0.84 [0.53–1.15]; Intercept: 0.37 [−0.15–0.88], $r^2 = 0.63$, $p < 0.01$). However, although roughly 85% of the studied sloth genera fall inside the area predicted by de IC model, the regression results are not consistent with the IC model. However, considering the plotted data (Text-fig. 4), it is evident that only one taxon falls well outside the IC model predicted area. In fact, the exclusion of this single taxon (*Octodontotherium*) significantly changes the obtained regression (Slope: 1.88 [1.37–2.39]; Intercept: −0.87 [−1.55–(−0.20)], $r^2 = 0.75$, $p < 0.01$), producing results largely consistent with the IC model.

Furthermore, when testing the existence of a similar pattern between the first three teeth (Text-fig. 5), the results show much less spread of the data (although, again, *Octodontotherium* falls considerably away from the rest of the taxa) as well as the lack of a pattern expected by the existence of IC (Slope: 1.11 [1.00–1.21]; Intercept: 0.05 [−0.16–0.27], $r^2 = 0.90$, $p < 0.01$).

Moreover, the mf2 roughly occupied 1/3 of the tooth row in all sloth families, but values in Mylodontidae were significantly lower ($p < 0.05$) than in the rest of the families while the values of the orophodontids were considerably higher than most other taxa (Tab. 3, Text-fig. 6).

Considering the spread of the data, as well as the results of the Tukey's post-hoc test, we tested the existence of different patterns among families. The results (Tab. 4) showed support for models taking mylodontids and orophodontids separately. The most supported model was the one with different regressions for mylodontids, orophodontids, and the rest of the sloths. In that case, the mylodontids showed a pattern consistent with the IC model, with a slope moderately higher than 2 (Slope: 2.88 [1.92–3.84]; Intercept: −1.52 [–2.05–(−0.99)], $r^2 = 0.70$, $p < 0.01$) which is consistent with the mf1 ≤ mf2 << mf3 pattern. In particular, the Scelidotheriinae *Catonyx* and *Valgipes* were placed outside the area predicted by the IC model, showing an mf1 > mf2 < mf3 configuration. On the other hand, the orophodontids showed a pattern inconsistent with the IC, with a slope slightly below 1 (Slope: 0.78 [0.63–0.93]; Intercept: 0.12 [−0.15–0.39], $r^2 = 0.69$, $p < 0.01$). Specifically, it is worth noting that the orophodontids represented the taxa that fell most distant from the area expected by the IC, with *Octodontotherium*, *Octodontobradys*, and *Baraguatherium* showing an mf1 < mf2 > mf3 configuration. The rest of the sloth taxa from the other families showed values almost consistent with the IC model and similar to values previously reported in other taxa where the IC model is present (see Tab. 5), with a slope below 2 but well above 1 (Slope: 1.57 [1.56–1.58]; Intercept: −0.54 [−0.71–(−0.37)], $r^2 = 0.80$, $p < 0.01$). Also, it is worth mentioning the placement of two Nothrotheriidae, *Aymaratherium* and *Mionothropus*, which fell well outside the predicted area with mf1 < mf2 > mf3 and mf1 > mf2 < mf3 configurations, respectively. Table 5 shows the comparisons of the obtained results in the regression analyses with the strict IC model prediction and previously obtained results in other mammalian groups.



Text-fig. 4. Macroevolutionary trends related to the IC model in the last three teeth of the six families of extinct sloths, as well as specimens of the "basal Megatherioidea", *Pseudoglyptodon*, and *Bradypus*. Dash-dot line (-.-) shows the regression including all data; solid line shows the regression after the exclusion of *Octodontotherium* (shown in the plot as a filled triangle).

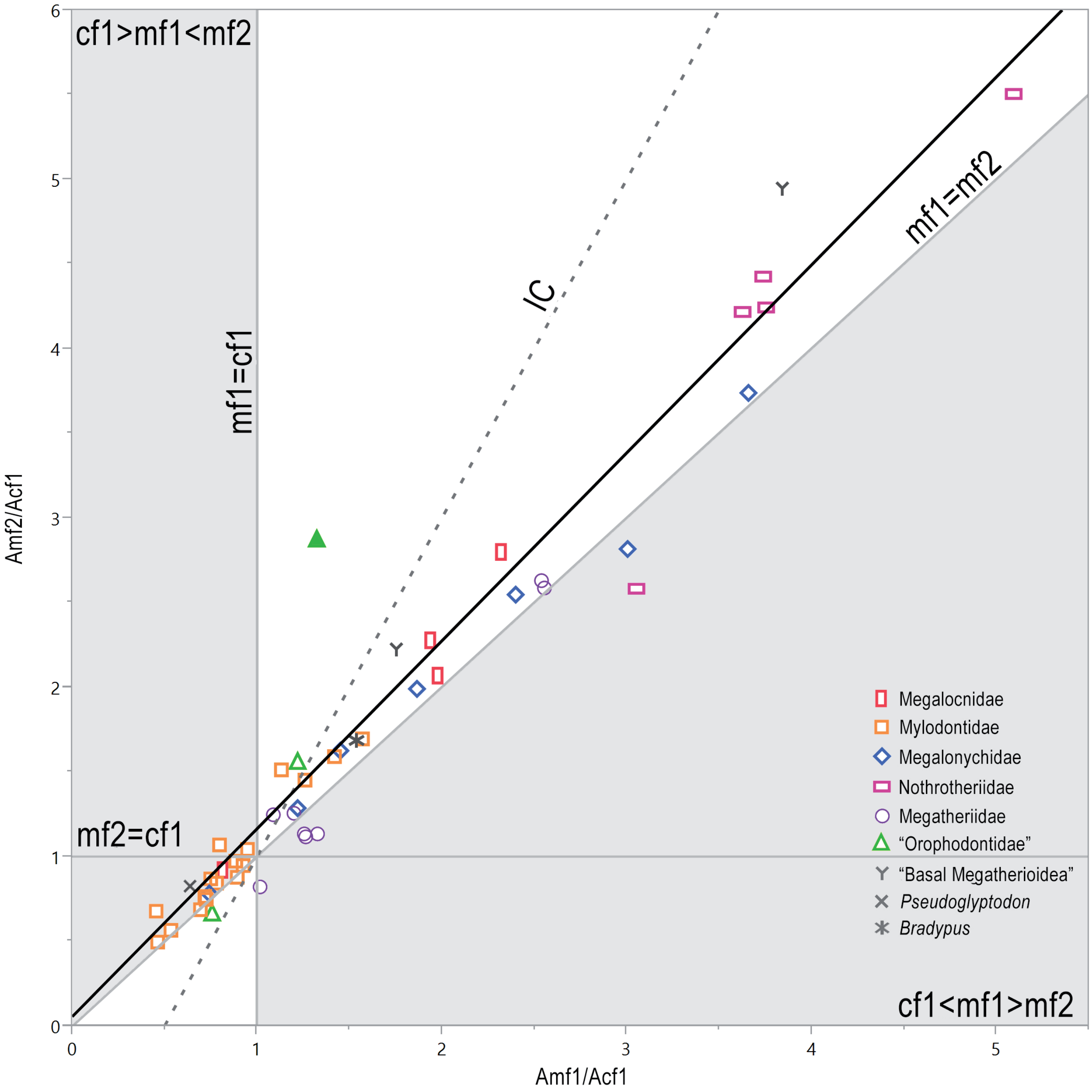
Discussion

The inhibitory cascade in sloths

The inhibitory cascade has been proven to be present in many groups of extant mammals, such as rodents, carnivorans, and primates, as well as extinct ungulates and Mesozoic basal mammals (Kavanagh et al. 2007, Polly 2007, Labonne et al. 2012, Wilson et al. 2012, Asahara 2013, Bernal et al. 2013, Halliday and Goswami 2013, Schroer and Wood 2015, Asahara et al. 2016, Evans et al. 2016, Gomes Rodrigues et al. 2017). In this work, we demonstrate that it is also present in at least one group of Xenarthrans, the Folivora, even with the many peculiarities in the dentition of the group: tooth loss, enamel loss, homodonty, and changes in the typical mammalian dental formula, among others.

In *Lestodon armatus*, our results show that the observed variability largely complies with the IC predictions. In this sloth, the last molariform is always the largest tooth in the series, but the mf1 and mf2 are similar in size, with some specimens with mf1 approximately equal to mf2. This variation could be related to ontogeny, with juvenile specimens having larger mf1, but mf2 and mf3 increasing in relative size during ontogeny. However, this pattern is not clear since many adult individuals present similarly sized mf1 and mf2 (Text-fig. 3) and the juvenile individuals were not clustered in any zone of the morphospace.

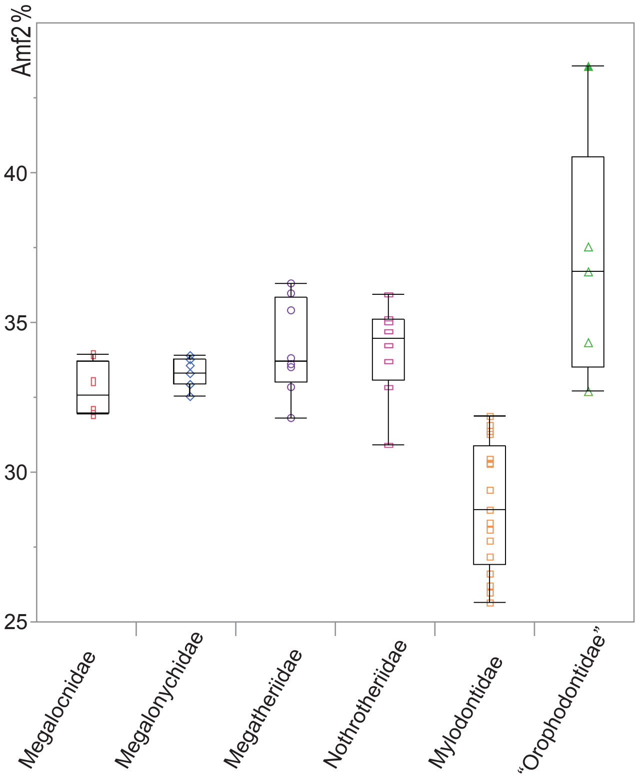
For all sloths, the existence of the IC in the last three teeth is largely supported in the clade. However, as mentioned



Text-fig. 5. Macroevolutionary trends related to the IC model in the first three teeth of the six families of extinct sloths, as well as specimens of the "basal Megatherioidea", *Pseudoglyptodon*, and *Bradypus*. Dashed line (- -) shows the regression including all data; solid line shows the regression after the exclusion of *Octodontotherium* (shown in the plot as a filled triangle).

before, the placement of one genus, *Octodontotherium*, as a clear outlier, required its exclusion to obtain significant results. Contrarily, a pattern consistent with the prediction of the IC model was not recovered for the first three teeth regardless of the first tooth morphology (caniniform or molariform).

Furthermore, significant differences were obtained between families when considering the area of mf2, with mylodontids and orophodontids respectively having an mf2 considerably smaller or larger than expected under the IC model. These differences were further explored after the evaluation of different slopes in these families. A slight departure from the strict prediction of the IC model was detected in the case of mylodontids. In this family, especially in mylodontines, a slope considerably larger than 2 was obtained between the molariform ratios, showing a pattern in which mf3 tends to be remarkably larger while mf1 and mf2 remain smaller and sometimes similar in size. In fact, some mylodontids, namely *Catonyx* and *Valgipes*, showed an mf1 > mf2 < mf3 configuration, which was proposed by Kavanagh et al. (2007) as the developmentally least likely phenotype to occur. For orophodontids, the slope was slightly lower than 1, showing a significant departure from thee IC model. However, as observed in Text-fig. 5, a pattern consistent with the IC model could be present in the first three teeth in orophodontids, but this cannot be confirmed with the current data due to the poor preservation or absence of cf1 in the specimens. These trends in orophodontids could be the result of different dental homologies in this clade compared with the rest of sloths. Nonetheless, a similar



Text-fig. 6. Boxplots showing the proportion of mf2 in relation to the sum of the occlusal area in the five families of extinct sloths.

pattern was previously reported in ursids, with evidence supporting the existence of a unique IC pattern in this group related to evolutionary changes in the expression or function of low diffusible inhibitory molecules (or their antagonists) affecting m2/m1, but not m3/m1 (Asahara et al. 2016). On the other hand, the observed slope after the exclusion of mylodontids and orophodontids showed that most sloths comply with the IC model predictions. Although the observed slope was slightly less steep than the strict prediction of the IC model, it was comparable to those observed in many mammalian groups, including the murine rodents originally studied by Kavanagh et al. (2007).

Even though the molariform loci of sloths seem not to be homologous with those of molars of other mammalian groups, the existence of the IC allows observing that the mechanisms described for other clades are probably also working during the development of the molariforms of sloths and constraining the evolution of relative tooth sizes. In this regard, it must be pointed out that only the mf3 of sloths would be homologous to a molar, particularly the m1 (Hautier et al. 2016), but the observed pattern across relative tooth sizes clearly indicates the influence of the front teeth on the hind teeth (i.e., the IC). On the other hand, premolars in mammals originate from back to front (unlike molars, which develop from front to back; Luckett 1993, van Nievelt and Smith 2005), and their influence over other teeth is not extensively studied.

Table 3. Proportion of the mf2 relative to the three last molariforms in sloths. Levels not connected by the same letters are significantly different ($p < 0.05$).

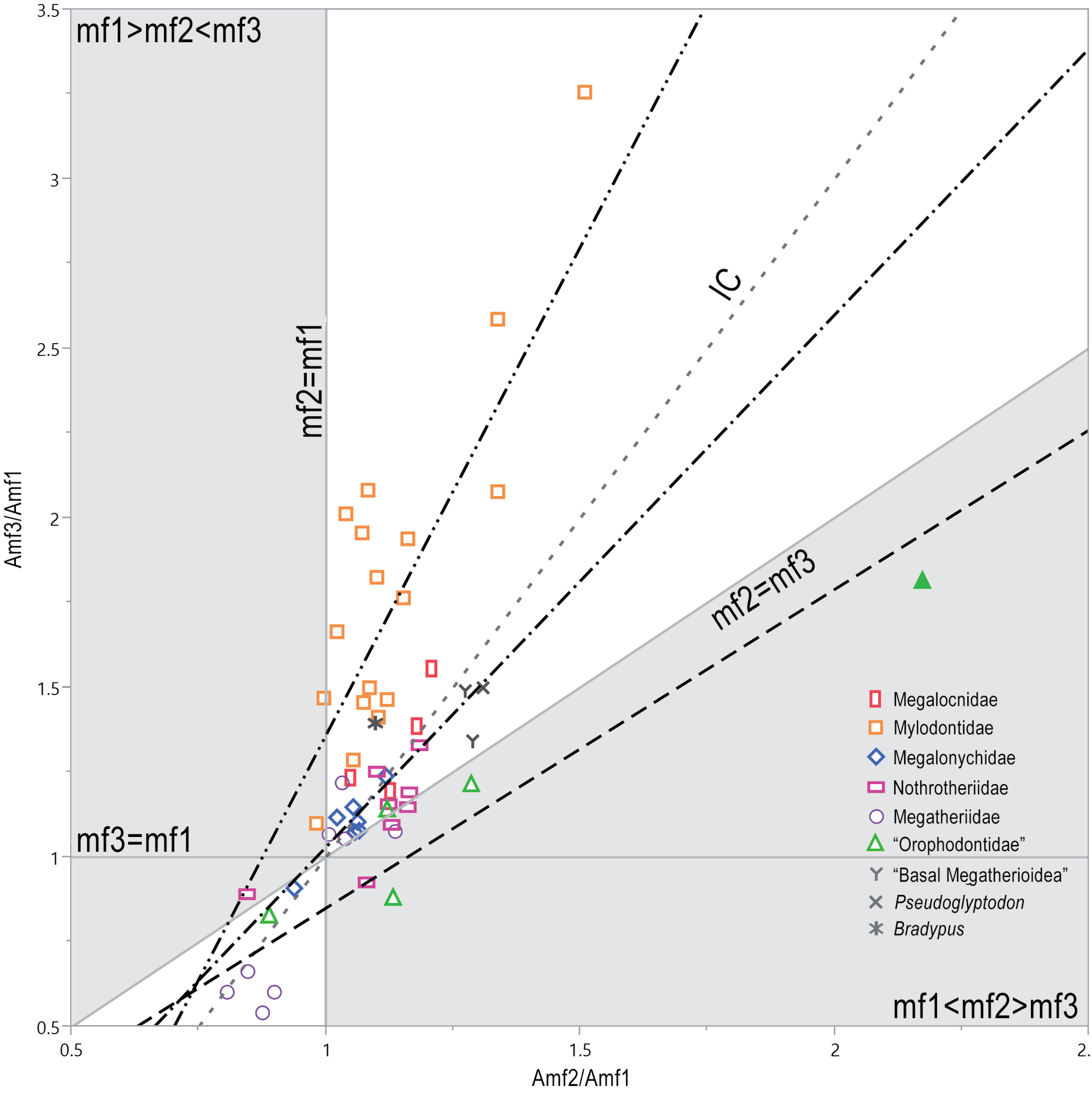
Taxon	Mean	SD	
All sloths	0.32	0.03	–
Megalocnidae	0.33	0.01	B
Megalonychidae	0.33	0.01	B
Megatheriidae	0.34	0.02	AB
Nothrotheriidae	0.34	0.02	AB
Mylodontidae	0.29	0.02	C
"Orophodontidae"	0.37	0.04	A

However, Labonne et al. (2012) found that the p4, when present, significantly influences the IC in rodents, constraining the development of m1 and affecting molars relative sizes. Furthermore, Evans et al. (2016) results indicate the existence of an expanded IC in hominins affecting all primary post-canine dentition, namely the deciduous premolars and molars. In most mammals, including hominins, these deciduous premolars are replaced by permanent premolars, so many studies are commonly based on this permanent dentition (Dahlberg 1945, Townsend and Brown 1981). However, sloths (and most xenarthrans) do not show tooth replacement and their mf1 and mf2 are probably homologous to the dp3 and dp4 of most mammals (see Hautier et al. 2016). Thus, the observed pattern in the molariforms ratios in sloths could be related to the existence of a similar IC pattern to that in hominins, in which the development of all present postcanine teeth is governed by the equilibrium between activation and inhibition between teeth, with the peculiarity that sloths would have lost their last two molars. Also, the clearly different IC pattern in mylodontids could be related to changes in inhibition and activation intensities along the cascade, in particular, an extreme activation of the mf3 development. However, considering the limited information regarding tooth development in fossil sloths, differences in tooth homologies in the case of mylodontids should not be ruled out. Moreover, given the fact that the first lower tooth (the caniniform in most sloths) seems to be a dp2, its potential effects over the IC should be taken into account, especially in cases where it shows a molariform morphology.

Finally, it must be mentioned that in most sloths the upper dentition has one more tooth, although according to the previously mentioned developmental studies the extra tooth is the first one and the last three molariforms still would be homologous to the dp3, dp4, and m1 of other mammals. However, in many sloths, including many in which the last lower tooth is the largest in the series, the last upper tooth is the smallest in the series. This apparent difference between upper and lower dentition regarding the trends in relative tooth sizes will be further studied in future research in order to explore differences between inhibition and activation intensities in both toothrows, a topic scarcely explored in previous works (Gomes Rodrigues et al. 2017).

IC and dietary adaptations in fossil sloths

Several authors reported variations in the IC model among taxa that related to different dietary adaptations. In rodents, an increase in the relative sizes of m2 and m3 led to an m1 = m2 = m3 configuration that was related to



Text-fig. 7. PGLS regressions for Mylodontidae, "Orophodontidae", and the rest of the sloths considered separately, Mylodontidae: dash double-dot line (-..-), "Orophodontidae": dash-dot line (-.-), rest of sloths: dash line (--).

more herbivorous diets (Kavanagh et al. 2007). Similarly, in canids, insectivorous and omnivorous taxa showed relatively smaller m1 and larger m2 and m3 than taxa with carnivorous habits (Asahara 2013). Moreover, a similar pattern was recovered by Halliday and Goswami (2013) for 135 genera from several extinct mammalian taxa, with more faunivorous taxa arranged in the bottom left of the morphospace and more herbivorous taxa in the top right.

In the case of sloths, the only proposed major group with dietary adaptations more related to bulk feeding or

Table 4. Model support of the regression models fitted to the sloth molariform ratios.

Model	AICc	ΔAICc	AICcw
All families considered separately	3.96	10.41	0.005
Mylodontidae and "Orophodontidae" considered separately	**−6.45**	**0**	**0.994**
Mylodontidae considered separately	32.15	38.6	< 0.001
"Orophodontidae" considered separately	7.88	14.33	0.001
All data	29.38	35.83	< 0.001

Table 5. PGLS regression analysis of sloth molariform ratios compared to previously published results in other mammalian groups.

	Slope	C.I. min	C.I. max	Intercept	C.I. min	C.I. max	r
IC model	2	–	–	0	–	–	1
Murinae (Kavanagh et al. 2007)	2.15	1.77	2.69	−1.22	−1.65	−0.93	0.74
Arvicolinae (Renvoisé et al. 2009)	1.39	1.21	1.56	−0.31	−0.41	−0.21	0.77
Carnivora (Asahara 2013)	0.59	0.49	0.74	−0.17	−0.22	−0.13	0.62
Astrapotheria (Wilson et al. 2012)	1.27	1.06	1.48	−0.29	−0.55	−0.04	0.91
Notoungulata (Wilson et al. 2012)	1.76	1.58	1.99	−0.66	−0.88	−0.46	0.81
Creodonta (Asahara et al. 2016)	2.57	1.30	7.25	−2.31	−8.59	−0.72	0.39
Dasyuromorphia (Asahara et al. 2016)	2.01	1.88	3.20	−1.31	−2.90	0.27	0.70
Folivora	0.84	0.53	1.15	0.37	−0.15	0.88	0.63
Folivora excluding *Octodontotherium*	1.88	1.37	2.39	−0.87	−1.55	−0.20	0.75
Mylodontidae	2.88	1.92	3.84	−1.52	−2.05	−0.99	0.70
“Orophodontidae”	0.78	0.63	0.93	0.12	−0.15	0.39	0.69
Folivora excluding Mylodontidae and “Orophodontidae”	1.57	1.56	1.58	−0.54	−0.71	−0.37	0.80

grazing are mylodontids, with some members of the family exhibiting these adaptations as early in the fossil record as the Oligocene (Bargo and Vizcaíno 2008, Shockey and Anaya 2011, Pujos et al. 2012). Considering our results, these adaptations could be related to the remarkable departure from the strict expected relative teeth sizes under the IC model, with mylodontids, especially mylodontines, showing an mf1 ≤ mf2 << mf3 configuration. In this case, the mf2 occupies ~29 % on average, while the mf3 occupies ~45 % of the molariform area.

On the other hand, all other sloths have been commonly interpreted as browsers, and they are mainly placed in the centre of the morphospace. However, it is particularly interesting that some megatheriids, specifically the largest megatheriines, were placed in the other extreme of the morphospace in the left bottom part of the graph, with almost all members having an mf1 > mf2 > mf3 configuration. As mentioned above, this part of the morphospace is associated with less herbivorous diets, with many omnivorous, insectivorous, and carnivorous taxa showing similar configurations. Interestingly, the giant megatheriine sloth *Megatherium americanum* from southern South America has so far been the only species with a proposed not strictly herbivorous diet (Fariña 1996, Fariña and Blanco 1996, Fariña and Varela 2018; see also Bargo 2001b). However, other evidence also suggests an herbivorous diet for this sloth (Green and Kalthoff 2015, Bocherens et al. 2017) and other developmental or morphofunctional reasons should not be discarded. In particular, the dental formula of megatheriines, with the first tooth having a molariform morphology in contrast to the caniniform present in most other sloths, could have affected the IC and should be further studied.

Conclusions

Our results show that, despite having extremely derived dentitions among mammals, sloths dental development is largely constrained by the same mechanisms acting in many other mammalian clades. At the same time, these mechanisms were important during the evolution of the group and, in part, produced the diversity of morphologies found in extinct and extant sloths. Moreover, important departures of the strictly expected morphology under the IC model seem to have allowed some sloths, specifically some mylodontids, a dentition arrangement better suited to grazing.

The previous findings regarding the development of teeth in extant sloths (Hautier et al. 2016), coupled to the analysis of the abundant extinct diversity of a group with only two extant genera, allowed us to test an important developmental model in a macroevolutionary context in a group of mammals in which the presence of the IC affecting tooth proportions would be considered improbable at first glance.

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