



# The Mysterious Loss of the Third Molar in the New World Monkey Family *Callitrichidae* and its Relationship to Phyletic Dwarfism

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## ABSTRACT

*Callitrichidae* is the smallest of five families of New World monkeys, descendants of African simians that colonized South America around 40 million years ago. Callitrichids, unlike other primates, do not develop third molars. It has been proposed that this is due to a crowding out event, whereby, over evolutionary time, a shortening cranium associated with decreasing body size pushed out the last molars on a tooth row that did not shrink as rapidly. This would create an equivalent relative area for chewing compared to non-callitrichid New World monkeys. After analyzing craniodental measurements of 143 New World monkey specimens, I found that callitrichids display an especially short postcanine row to body size ratio. A direct link between reduced body mass and third molar loss in callitrichids remains unsubstantiated, although current research suggests they may be related via an underlying genetic mechanism. Researching these associated genes may have implications for human health.

## INTRODUCTION

Among the five New World monkey, or platyrrhine, families, which include Aotidae, Atelidae, Cebidae, Pitheciidae, and Callitrichidae, only the last is believed to have experienced phyletic dwarfing, or decreasing in size over evolutionary time.<sup>1</sup> Research on phyletic dwarfing has usually concerned islands. However, its occurrence on larger land masses may be a more common phenomenon than much of the literature suggests, with evolutionary episodes happening independently in a few mammalian lineages besides callitrichids.<sup>2</sup> Reduced body size is part of a suite of distinctive features that define callitrichids: higher rates of twinning, the presence of claws, and the absence of third molars and hypocenes also distinguish this family.<sup>1</sup> However, due to an incomplete fossil record and relatively recent resolution in the phylogeny of platyrrhines, it is unclear whether these characters evolved synchronously during one evolutionary event or during parallel episodes of body size reduction. Either way, morphological diversification in callitrichids appears to have resulted from a strong positive selection on size, so size is an adaptive trait in this family.<sup>2</sup>

The sparse fossil record of callitrichids from the Plio-Pleistocene has limited the scope of research on the climatic and ecolog-

ical conditions that were prevalent during the evolution of their dwarfism. Early research in this topic posited that no minimum date can be set for the occurrence of one or several dwarfing episodes. However, a likely location for these events, the forests of continental South America, is supported by the current and likely historic habitat distribution of callitrichids. While larger platyrrhines are found principally in gallery forest, the smaller ones, particularly the callitrichids, are found in dense secondary growth and scrub forest. Possibly, times of dryness and of reduced and widely separated forest regions, in concert with the normal perturbations of the tropical environment, may have led to limitations of resources. This may have favored smaller species that would rely on less food and territory, then allowing the callitrichid population to boom after these resources replenished. Tooth morphology could have diverged as an adaptation to dietary specialization either during or subsequently to this period.<sup>2</sup>

It is possible, then, that understanding the postcanine dentition of callitrichids can shed light on an evolutionary relationship between their dwarfism and third molar loss. The focus specifically on postcanine dentition, the molars and premolars, is appropriate, as its genetic regulation and development are separate from those of anterior dentition.<sup>3</sup> As well, postcanine dentition is known

to be correlated with body size across primates.<sup>4</sup> Generally, dwarfed lineages have been shown to exhibit different ontogenetic scaling, the change in the size of one feature relative to another during early evolutionary and embryonic development, from the normal interspecific trend.<sup>5</sup> Gould<sup>6</sup> suggested that in dwarfed lineages, body size decreases far more rapidly than the postcanine dentition. For example, an increase in relative molar size in Pleistocene marsupial lineages was associated with decreasing body size.<sup>7</sup> This scaling phenomenon, whereby an organ grows or shrinks more slowly than the rest of the body, in a lifespan or over evolutionary time, is known as negative allometry.<sup>1</sup> Callitrichids, not unusual among primate families in their tooth eruption patterns at birth, were assumed to follow this trend.<sup>8</sup> Hence, Gould hypothesized that the oversized molar battery relative to a reducing mandible may have led to the crowding out and loss of their third molar. This would allow for a functional chewing surface that takes up a portion of their skull that is roughly equivalent to non-callitrichid platyrrhines. A 1993 study suggested, on the other hand, that the postcanine row of callitrichids takes up significantly less area of the entire cranium than that of non-callitrichid platyrrhines in three of four genera tested, the exception being in the *Leontopithecus rosalia* species.<sup>9</sup> A small handful of species that dwarf have been shown to lack this negative allometry.<sup>7</sup> If callitrichids do not fit this trend as well, it may be related to their rare change in ontogeny, or development, whereby prenatal growth rate was slowed down. This would explain how their body size was reduced.<sup>10</sup> While developmental genetics has been shown to inform craniofacial and dental morphology across a variety of mammalian species,<sup>11</sup> the type of body size reduction seen in callitrichids is likely a rarity among mammals apart from domestic dog breeds, among which postnatal growth rates vary little.<sup>12</sup> Further, it has been suggested that dwarfism in callitrichids is associated singularly with these changes in prenatal growth rates rather than the duration of gestation, postnatal growth duration, or postnatal growth rates. The exception to this is *C. pygmaea*, whose extremely small body mass is probably caused by a lagging of both prenatal and postnatal growth rates, suggesting that their accelerated sexual maturation relative to the rest of their development could have played a role in the evolution of this species.<sup>2</sup>

I hypothesized that the loss of the third molar in callitrichids is correlated with a shortening of the facial skeleton that over evolutionary time, forced out the last molar. This would be consistent with the crowding out hypothesis and the general trend in allometry seen in dwarfing lineages. I also hypothesized that callitrichids' unique ontogeny would be irrelevant in affecting this ubiquitous trend. Thus, there would be no significant difference between the relative size of the postcanine tooth row, both maxillary and mandibular, of callitrichids when compared to non-callitrichid platyrrhines. The Plavcan and Gomez study that rejected this crowding out hypothesis tested a sample of 18 species, including four callitrichid species. This represented a smaller species richness than the 42 species, including five callitrichid species, used by my study. I suspected that the lower species di-

versity of the Plavcan and Gomez study may have limited its comparative power, with the postcanine row trend only becoming visible when platyrrhine families are studied more broadly.

## MATERIALS AND METHODS

### Materials

To evaluate relative postcanine tooth row sizes between callitrichids and non-callitrichid platyrrhines, I compared ratios of postcanine row length to various measurements of cranial length between these two groups. Instead of measuring body volume directly, I compared the tooth row with skull measurements that are known to be strongly correlated with body size and which are more feasible to measure.<sup>13</sup>

I collected data from 157 platyrrhine skulls in total, comprised of 34 skull photographs of specimens from the Smithsonian National Museum of Natural History, 106 skulls from the Museum of Vertebrate Zoology mammalogy research collection, and 17 skulls from the California Academy of Sciences mammalogy research collection. Of these 157 specimens, the 143 adults, defined as having fully erupted dentitions, were analyzed. This way, I knew intraspecific variation would not be confounded by variable stages in development. The sample spanned all five families of platyrrhines, consisting of 57 callitrichids, 22 cebids, 14 aotids, 21 pitheciids, and 29 atelids. In total, there were 16 genera and 42 species included in the study.

### Data Collection Methods

I measured the upper and lower postcanine tooth row lengths on both sides of the face, mandible lengths, cranium lengths, and calvarium, or skullcap, lengths, of every museum specimen. I used Mitutoyo digital calipers, and performed three separate trials for all seven measurements on each specimen (Figures 1-3). I conducted photograph measurements on ImageJ version 1.48<sup>14</sup> with a standardized protocol, using the same landmarks as on the museum specimens. However, I did not gather calvarial measurements from the photograph specimens since dorsal and lateral views of the skulls were unavailable.

### Analytical Methods

I generated all statistical analyses in R, version v3.1.2.<sup>16</sup> I averaged the measurements from the three different trials for each specimen after determining that the differences in the measurements were not statistically significant. To resolve concerns about possible bias that could have arisen from the two different measurement methods, I ensured that photograph and caliper measurements gleaned from 10 randomly selected platyrrhine skull specimens from the Museum of Vertebrate Zoology were insignificant in their differences. I subsequently collapsed the two data sets (Table 1).

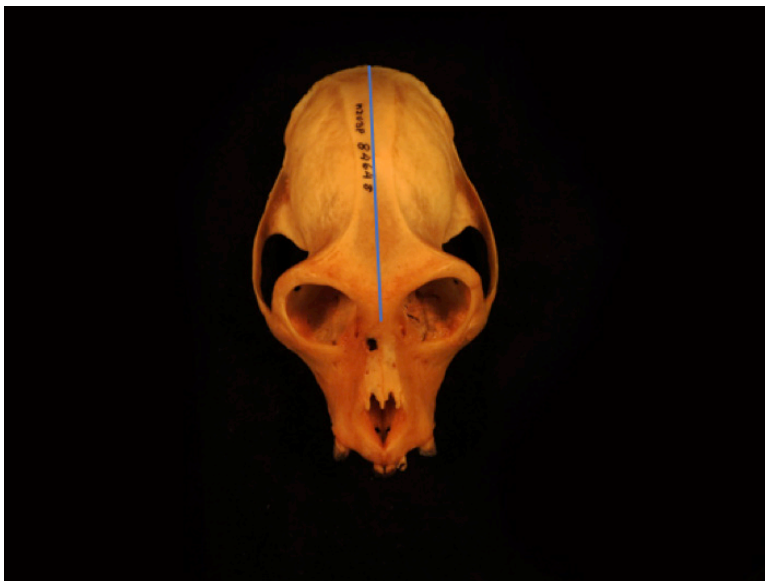
After verifying that postcanine row length side differences were insignificant, I averaged the two right and left postcanine tooth rows of the maxilla as an upper tooth row, and the two mandibular tooth rows as a lower tooth row. I calculated



**Figure 1.** Green line shows visual of cranial length measurement. I measured cranium on the ventral side of the skull, from the front of the alveolus between the central incisors to the midpoint of the occipital crest where the parietal midline suture begins. The blue line shows visual of postcanine tooth row length. I measured this from the most anterior point of the second premolar to the most posterior point of the most posterior molar, either second or third. Photograph represents a sampled specimen of the species *Leontopithecus rosalia*. Specimen number is 588174 from the Smithsonian Institution National Museum of Natural History.



**Figure 2.** Blue line shows visual of mandible length measurement. I took mandibular length as the path from the superior infradentale between the central incisors to the midpoint of the superior left condyle of the mandible (15). Photograph represents a sampled specimen of the species *Leontopithecus rosalia*. Specimen number is 588174 from the Smithsonian Institution National Museum of Natural History.

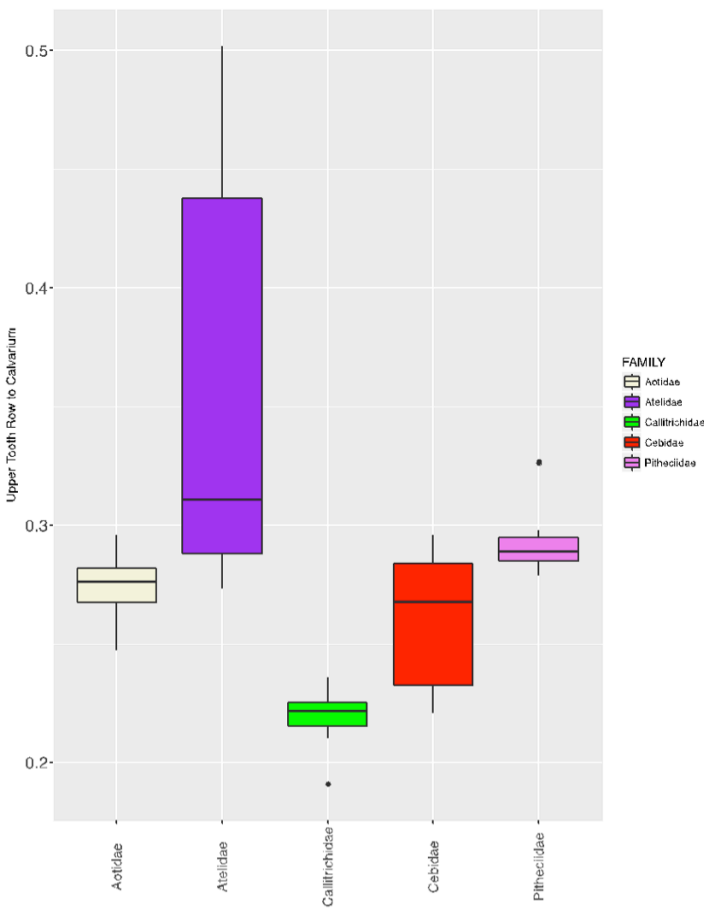


**Figure 3.** Blue line shows visual of calvarium length measurement. I measured calvarium length from the midpoint of the suture dividing the nasal and frontal bones to the midpoint of the occipital crest, the suture dividing the occipital and parietal bones, where the parietal midline suture begins. This was conducted laterally with the calipers placed parallel to the occlusal plane of the teeth rather than perpendicular as in the other measurements. This was due to its ability to generate reproducibility and consistency given the shapes of the skulls. Photograph represents a specimen of the species *Alouatta guariba clamitans* not sampled in this study. Specimen number is 84648 and is from the Zoology Museum of the University of São Paulo.

Family	Statistic	Right Maxillary Postcanine Length (mm)	Left Maxillary Postcanine Length (mm)	Right Mandibular Postcanine Length (mm)	Left Mandibular Postcanine Length (mm)	Mandible Length (mm)	Calvarium Length (mm)	Cranial Length (mm)
<i>Aotidae</i>	Sample Size	11	12	11	12	12	14	14
	Median	14.13	14.10	15.93	15.82	38.34	51.19	60.19
	Mean	14.20	14.16	15.82	15.77	38.71	51.73	60.29
	SD	0.52	0.45	0.44	0.46	1.24	2.20	1.54
<i>Atelidae</i>	Sample Size	20	20	25	25	29	29	29
	Median	24.30	24.81	28.11	28.01	72.64	79.81	106.13
	Mean	26.63	27.60	30.43	30.91	75.68	78.96	108.54
	SD	4.29	5.01	5.69	5.86	9.61	4.94	6.56
<i>Callitrichidae</i>	Sample Size	53	52	52	54	53	23	56
	Median	8.98	8.91	10.38	10.44	30.70	41.19	44.29
	Mean	9.36	9.35	10.74	10.73	31.01	39.36	45.30
	SD	1.65	1.63	1.79	1.74	4.17	5.26	5.88
<i>Cebidae</i>	Sample Size	12	15	17	16	22	21	22
	Median	16.31	20.38	23.75	22.92	55.08	68.91	84.79
	Mean	16.59	17.71	20.48	20.15	49.66	66.34	80.36
	SD	4.29	4.35	4.80	4.80	12.04	10.25	14.12
<i>Pitheciidae</i>	Sample Size	17	15	18	16	19	21	21
	Median	15.30	15.44	17.44	17.37	41.53	53.22	62.14
	Mean	16.86	16.94	18.91	18.96	47.40	56.44	68.99
	SD	2.31	2.47	2.81	2.96	9.81	7.21	12.370

**Table 1 (top).** Sample sizes and descriptive statistics for all traits measured for all five families.

**Figure 4 (bottom).** Boxplot shows ratios of upper postcanine tooth row lengths relative to calvarium lengths across families. Upper and lower postcanine rows compared to all cranial measurements showed similar trends, with callitrichids having relatively smaller postcanine tooth rows than all other families.



the ratio of the upper and lower tooth rows to the mandible length, calvarium length, and cranium lengths to standardize the tooth row data. I ran correlations to see how strongly the average upper and lower tooth row lengths were correlated with mandible, calvarium, and cranial lengths, and to determine how strong the correlations among mandible, calvarium, and cranial lengths were. Since all skull measurements are related to body size and were expected to be highly correlated with each other, the latter correlations acted as a control.<sup>13</sup>

With the callitrichid species *L. rosalia* and *C. pygmaea*, I performed separate ANOVA analyses. In one, I treated *C. pygmaea* as a family to compare its ratios to those of all the other callitrichids, as well as to those of the other platyrrhine families. This was to examine whether their unique ontogeny and even more dramatic dwarfing may be associated with significant negative allometry even relative to other callitrichids. In the other, I did the same for *L. rosalia*, also to learn if they displayed uniquely strong negative allometry. This was based on the findings of Plavcan and Gomez that *L. rosalia* was the only callitrichid to not display a relatively smaller postcanine row compared to non-callitrichid platyrrhine species.<sup>2,8</sup> In this case, I wanted to investigate the possibility that only this genus's lineage shows negative allometry. Besides these examples, results were analyzed across entire families rather than among genera or species.

## RESULTS

Correlations were scaled between 0 and 1, with 1 representing perfect correlation. The postcanine tooth row lengths compared to the mandible lengths were 0.982 and 0.980 for the top and bottom, respectively. The postcanine tooth row lengths compared to the calvarium lengths were 0.869 and 0.863 for the top and bottom, and when compared to the cranial lengths, were 0.961 and 0.958. The mandible and calvarium

lengths were correlated at 0.898, the mandible and cranial lengths at 0.976, and the calvarium and cranial lengths at 0.969. All the traits were significantly correlated with each other.

Callitrichids showed significantly shorter maxillary and mandibular postcanine tooth rows relative to the three cranial measurements when compared to the other platyrrhine families (Figure 4; Table 2). *L. rosalia* displayed a significantly larger postcanine row relative to skull length when compared to other callitrichids. When compared to non-callitrichid platyrrhine families, however, *L. rosalia* exhibited a significantly smaller postcanine ratio relative to at least one skull measurement (Table 3). There were no significant differences between *C. pygmaea* and other callitrichids in their postcanine row relative to their skull lengths (Table 4).

## DISCUSSION

Tooth row length's significant correlations with the mandible length, calvarium length, and cranial length, across families, confirm that a strong relationship exists between tooth row length and body size. Slightly lower correlations between the tooth row lengths and calvarium lengths may be due to the high quantity of missing calvarium data from the photograph measurements rather than to a weaker relationship.

My study demonstrates that the postcanine row of callitrichids is shorter relative to the various skull lengths when compared to non-callitrichid platyrrhines, indicating that their postcanine row consumes a smaller region of their skull. My study's results are consistent with those of the Plavcan and Gomez study. In interpreting these results, Plavcan and Gomez accepted Gould's assumption that phyletic dwarfism must be associated with ontogenetic scaling. In this instance, ontogenetic scaling was expected to manifest in the usual trend of negative allometry, or larger tooth area relative to decreased body size. Plavcan and Gomez, thus, could not assert callitrichids underwent phyletic dwarfism. Their study claimed that the unique callitrichid traits of higher twinning rates, claws, third molar loss, and no hypocones are not even suggestive of a dwarfing event or a series of such events. They argued that given the trend of third molar size reduction in non-dwarfed platyrrhines, the loss of this tooth in callitrichids may represent a simple continuation of a general trend unrelated to body size reduction. Plavcan and

Family Comparison	Upper Average to Mandible	Lower Average to Mandible	Upper Average to Calvarium	Lower Average to Calvarium	Upper Average to Cranium	Lower Average to Cranium
Atelidae-Aotidae	0.847	1.000	0.000	0.000	0.229	0.106
Callitrichidae-Aotidae	0.000	0.000	0.006	0.128	0.000	0.006
Cebidae-Aotidae	0.847	0.950	0.887	1.000	0.125	0.878
Pitheciidae-Aotidae	0.417	0.904	0.817	0.749	0.989	0.928
Callitrichidae-Atelidae	0.000	0.000	0.000	0.000	0.000	0.000
Cebidae-Atelidae	1.000	0.906	0.000	0.000	0.000	0.001
Pitheciidae-Atelidae	0.879	0.780	0.000	0.001	0.404	0.343
Cebidae-Callitrichidae	0.000	0.000	0.059	0.087	0.309	0.061
Pitheciidae-Callitrichidae	0.000	0.000	0.000	0.001	0.000	0.000
Pitheciidae-Cebidae	0.941	0.271	0.210	0.620	0.020	0.291

Family Comparison with Cebuella	Upper Average to Mandible	Lower Average to Mandible	Upper Average to Calvarium	Lower Average to Calvarium	Upper Average to Cranium	Lower Average to Cranium
Atelidae-Aotidae	0.913	1.000	0.000	0.000	0.300	0.145
Callitrichidae-Aotidae	0.000	0.000	0.017	0.307	0.000	0.014
Cebidae-Aotidae	0.912	0.950	0.941	1.000	0.170	0.934
Cebuella-Aotidae	0.000	0.000	0.164	0.342	0.024	0.110
Pitheciidae-Aotidae	0.516	0.904	0.891	0.836	0.997	0.966
Callitrichidae-Atelidae	0.000	0.000	0.000	0.000	0.000	0.000
Cebidae-Atelidae	1.000	0.906	0.000	0.000	0.000	0.002
Cebuella-Atelidae	0.000	0.000	0.000	0.000	0.000	0.000
Pitheciidae-Atelidae	0.935	0.780	0.001	0.002	0.501	0.433
Cebidae-Callitrichidae	0.000	0.000	0.131	0.249	0.458	0.117
Cebuella-Callitrichidae	1.000	1.000	1.000	0.994	0.995	0.988
Pitheciidae-Callitrichidae	0.000	0.000	0.000	0.006	0.000	0.000
Cebuella-Cebidae	0.000	0.000	0.467	0.321	0.656	0.348
Pitheciidae-Cebidae	0.974	0.271	0.280	0.722	0.029	0.374
Pitheciidae-Cebuella	0.001	0.001	0.018	0.038	0.005	0.015

Family Comparison with Leontopithecus	Upper Average to Mandible	Lower Average to Mandible	Upper Average to Calvarium	Lower Average to Calvarium	Upper Average to Cranium	Lower Average to Cranium
Atelidae-Aotidae	0.865	1.000	NA	NA	0.230	0.125
Callitrichidae-Aotidae	0.000	0.000	NA	NA	0.000	0.001
Cebidae-Aotidae	0.864	0.941	NA	NA	0.118	0.926
Leontopithecus-Aotidae	0.001	0.002	NA	NA	0.968	0.956
Pitheciidae-Aotidae	0.383	0.888	NA	NA	0.996	0.962
Callitrichidae-Atelidae	0.000	0.000	NA	NA	0.000	0.000
Cebidae-Atelidae	1.000	0.891	NA	NA	0.000	0.002
Leontopithecus-Atelidae	0.008	0.000	NA	NA	0.045	0.013
Pitheciidae-Atelidae	0.897	0.750	NA	NA	0.423	0.402
Cebidae-Callitrichidae	0.000	0.000	NA	NA	0.044	0.017
Leontopithecus-Callitrichidae	0.000	0.024	NA	NA	0.001	0.088
Pitheciidae-Callitrichidae	0.000	0.000	NA	NA	0.000	0.000
Leontopithecus-Cebidae	0.022	0.000	NA	NA	0.643	1.000
Pitheciidae-Cebidae	0.957	0.231	NA	NA	0.015	0.344
Pitheciidae-Leontopithecus	0.139	0.015	NA	NA	0.775	0.523

**Table 2 (top).** ANOVA for ratio values of specimens across families. Shaded cells are significant at  $p < .05$ .

**Table 3 (middle).** ANOVA for ratio values of specimens across families, including "family" *Cebuella*. Shaded cells are significant at  $p < .05$ .

**Table 4 (bottom).** ANOVA for ratio values of specimens across families, including "family" *Leontopithecus*. Shaded cells are significant at  $p < .05$ .

Gomez stated that while tooth size is determined early in ontogeny and seems less affected by systemic growth, body size reduction appears in truncating late growth. They suggested that callitrichids are likely under the effects of longer gestation periods rather than being dwarfed via ontogenetic scaling. Their work could not, on the other hand, disprove that callitrichids underwent body size reduction over time. Plavcan and Gomez claimed that their linear regression results would differ depending on whether the size reduction in callitrichids was rapid or gradual, and that the allometry of callitrichids is associated with a gradual decrease in body size over time.

Plavcan and Gomez reasoned that it was unlikely that cranium shortening and the subsequent lack of occlusal space caused the last molar to be pushed out of the postcanine tooth row. The work performed by Cai et al.<sup>17</sup> also lends support to the rejection of Gould's hypothesis; it posited that tooth size and number might be regulated independently, and that changes in the number of molars can take place without affecting the molar area. There would be no selective benefit for the third molar to be forced out due to a lack of occlusal space, if the overall molar area does not necessarily change relative to the cranium and jaw.

My study, from the Plavcan and Gomez perspective, provides an even stronger argument for callitrichids not being phyletic dwarfs. *L. rosalia* and all other callitrichids in my sample show significantly smaller postcanine to cranial length ratios compared to non-callitrichid platyrrhines, reinforcing a lack of negative allometry and ontogenetic scaling in this family. Plavcan and Gomez showed that only *L. rosalia* consistently fell above the regression lines comparing tooth area to cranial size, which indicates that its postcanine row, compared to non-callitrichid platyrrhine species, was not significantly smaller relative to its cranium size. However, *L. rosalia*, being the largest callitrichid, still did not provide sufficient evidence to support Gould's dwarfism hypothesis.

The conclusions of Plavcan and Gomez, however, become questionable when considering the perspective of Montgomery and Mundy. Their 2013 study realized species-level mathematical analyses on gestation length, prenatal growth, prenatal growth rate, and age at sexual maturity, a measure of the length of postnatal growth and growth rate, in callitrichids. In contrast to what Plavcan and Gomez proposed, episodes of body mass reduction in callitrichids occurred concurrently with shifts in prenatal growth rate, and gestation length is not significantly shorter in callitrichids than in other primates, including non-callitrichid platyrrhines. Montgomery and Mundy also offered an alternative type of ontogenetic scaling that supported the dwarfism hypothesis. Using ancestral-state reconstruction, they discovered that the average rates of body mass reduction in callitrichids are somewhat lower than the well-studied episodes of island dwarfism in Pleistocene mammals. The timescale considered in these studies are typically in the orders of thousands of years, rather than millions. The percentage change in body size of callitrichids is therefore equal to or greater than most examples of dwarfism. The rate of change of adult body mass in callitrichids is like that of horses, which evolved over similar time lengths.

My study's additional comparison with *C. pygmaea*, the species that defies the Montgomery and Mundy trend in also possessing a lag in postnatal growth rate, suggests that its special ontogeny does not seem to inform its postcanine tooth row length. This raises a further research question as to whether callitrichid dentition and third molar disappearance share an underlying genetic link only with their stalled prenatal growth rate. These may not be influenced by the addition of a slower postnatal growth rate, as seen in *C. pygmaea*.

We do not know what caused the third molar in callitrichids to vanish, nor do we know why their bodies shrank over time. The area of callitrichids' first molar relative to the remainder of their molar row is consistent with the expected ratios from the proportion of genetic activators and inhibitors that regulate primate molar development. However, this does not explain their third molar's agenesis, or failure to grow in the embryonic stage. Genetic patterning mechanisms around third molar suppression are likely to be best understood by perusing the modulation of tooth patterns and associated genes around third molar agenesis. It is possible that the suppression and agenesis third molar may be achieved by altering existing and highly conserved genetic pathways.<sup>18</sup>

## CONCLUSION

Moving forward, studies on extant human populations and other non-human primates might also elucidate the mechanisms of tooth agenesis. The failure to develop normal teeth is common in modern humans, typically affecting the teeth that develop last in each tooth class of the secondary dentition, the set of 32 permanent teeth that erupt in childhood and last until old age. The agenesis of the third molar is the most frequent. The greater susceptibility shown by the last developing teeth suggests an overall reduction of odontogenic potential. This could be produced by heterozygous loss of function mutations that reduce the gene dose during the final stages of tooth development.<sup>19</sup> Thus, research on genetic patterning in callitrichids could have implications for understanding and correcting common agenesis-related mutations in humans.

To date, mutations in many genes have been identified in human families with tooth agenesis. Some of them, such as mutations in *MSX1* and *PAX9*, are commonly associated with reduced dimensions, shortened roots, and simplified form.<sup>11</sup> Whether the same genes are involved in the loss of the third molar in callitrichids is still a subject of research. Only one study has evaluated the *PAX9* gene in platyrrhines, in the genera *Callithrix*, *Saimiri*, and *Aotus* of the *Cebidae* family. The results obtained showed that these species share mutations in this gene that change three of the amino acids produced compared to humans and apes, except for *Aotus*, which creates two of these changed amino acids.<sup>20</sup> It is unclear at this point if this gene is having a similar effect in these cebid species as it is in humans. Further studies would need to discern any polymorphisms, sequence differences, or gene dose mutations in the *PAX9* gene of callitrichids and uncover if these are associated

with callitrichids' complete loss of their third molar. In fact, studies evaluating a larger number of genes known to regulate molar development are required to understand the specific molecular mechanisms responsible for dental variation within the platyrrhine clade. This could help clarify whether third molar agenesis is linked to genes known to affect body size.

Ultimately, my study supports an association between reduction in tooth number and phyletic dwarfism in callitrichids. Nevertheless, a lack of room in the cranium or mandible is unlikely to be responsible for an adaptive loss of their third molar. The disappearance of the third molar, then, is probably not a product of selection on a phenotype or dietary specialization. Rather, it seems to be related to shared genetic patterning effects underlying body mass, cranium length, and postcanine tooth row length.

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## REFERENCES

1. Ford, S.M., Callitrichids as phyletic dwarfs, and the place of the *Callitrichidae* in Platyrrhini, *Primates*, 21.1, 31-43, 1980.
2. Montgomery, S.H., and Mundy, N.I., Parallel episodes of phyletic dwarfism in Callitrichid and Cheirogaleid primates, *Journal of Evolutionary Biology*, 26.4, 810-819, 2013.
3. Hlusko, L.J., Sage, R.D., and Mahaney, M.C., Modularity in the mammalian dentition: mice and monkeys share a common dental genetic architecture, *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 316.1, 21-49, 2011.
4. Jiménez-Arenas, J.M., Pérez-Claros, J.A., Aledo, J.C., and Palmqvist, P., On the relationships of postcanine tooth size with dietary quality and brain volume in primates: implications for hominin evolution, *BioMed Research International*, 2014.
5. Shea, B.T., and Gomez, A.M., Tooth scaling and evolutionary dwarfism: An investigation of allometry in human pygmies, *American Journal of Physical Anthropology*, 77.1, 117-132, 1988.
6. Gould, S.J., Allometry in primates, with emphasis on scaling and the evolution of the brain, *Contributions to Primatology*, 5, 244-292, 1975.
7. Marshall, L.G., and Corruccini, R.S., Variability, evolutionary rates, and allometry in dwarfing lineages, *Paleobiology*, 4.2, 101-119, 1978.
8. Smith, T.D., Muchlinksi, M.N., Jankord, K.D., et al., Dental maturation, eruption, and gingival emergence in the upper jaw of newborn primates, *Anatomical Records (Hoboken)*, 298.12, 2098-2131, 2015.
9. Plavcan, J.M., and Gomez, A.M., Relative tooth size and dwarfing in callitrichines, *Journal of Human Evolution*, 25.3, 241-245, 1993.
10. Garber, P.A., Vertical clinging, small body size, and the evolution of feeding adaptations in the *Callitrichinae*, *American Journal of Physical Anthropology*, 88.4, 469-482, 1992.
11. Bernal, V., Gonzalez, P.N., and Perez, S.I., Developmental processes, evolvability, and dental diversification of new world monkeys, *Evolutionary Biology*, 40.4, 532-541, 2013.
12. Rizk, O.T., Insight into the genetic basis of craniofacial morphological variation in the domestic dog, *Canis familiaris*, Dissertation, 2012.
13. Sears, K.E., Finarelli, J.A., Flynn, J.J., and Wyss, A.R. Estimating body mass in New World "monkeys" (Platyrrhini, Primates), with a consideration of the Miocene platyrrhine, *Chilecebus carrascoensis*, *American Museum Novitates*, 1-29, 2008.

14. Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <https://imagej.nih.gov/ij/>, 2016.
15. Kanazawa, E., and Rosenberger, A.L., Reduction index in the upper M2 in marmosets, *Primates*, 29.4, 525-533, 1988.
16. R Core Team., R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, <http://www.R-project.org/>, 2016.
17. Cai, J., Cho, S.W., Kim, J.Y., et al., Patterning the size and number of tooth and its cusps, *Developmental Biology*, 304.2, 499-507, 2007.
18. Tummers, M., and Thesleff, I., The importance of signal pathway modulation in all aspects of tooth development, *Journal of Experimental Zoology Part B, Molecular and Developmental Evolution*, 312B.4, 309-319, 2009.
19. Nieminen, P., Genetic basis of tooth agenesis, *Journal of Experimental Zoology*, 312B.4, 320-342, 2009.
20. Pereira, T.V., Salzano, F.M., Mostowska, A., et al., Natural selection and molecular evolution in primate PAX9 gene, a major determinant of tooth development, *Proceedings of the National Academy of Sciences*, 103.15, 5676-5681, 2006.

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