Evolutionary implications of dental anomalies in bats

Diego A. Esquivel, Renan Maestri, and Sharlene E. Santana

1Programa de Pós-Graduação em Biologia Animal, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS 91501–970, Brazil
2Fundación Kurupira, Bogotá, DC 110921, Colombia
3E-mail: diegodaem@gmail.com
4Department of Ecology, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS 91501–970, Brazil
5Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, Illinois 60605
6Department of Biology, University of Washington, Seattle, Washington 98195
7Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington 98195

Received July 20, 2020
Accepted February 17, 2021

The gain or loss of anatomical features is an important mechanism of morphological evolution and ecological adaptation. Dental anomalies—the loss or gain of teeth—are widespread and a potential source of craniodental specialization among mammals, yet their macroevolutionary patterns have been rarely explored. We present the first phylogenetic comparative study of dental anomalies across the second largest mammal Order, Chiroptera (bats). We conducted an extensive literature review and surveyed a large sample of museum specimens to analyze the types and prevalence of dental anomalies across bats, and performed phylogenetic comparative analyses to investigate the role of phylogenetic history and dietary specialization on incidence of dental anomalies. We found dental anomalies have a significant phylogenetic signal, suggesting they are not simply the result of idiosyncratic mutations or random developmental disorders, but may have ancestral genetic origins or result from shared developmental pathways among closely related species. The incidence of dental anomalies was not associated with diet categories, suggesting no effect of craniodental specialization on dental anomalies across bats. Our results give insight into the macroevolutionary patterns of dental anomalies in bats, and provide a foundation for investigating new hypotheses underlying the evolution of dental variation and diversity in mammals.

KEY WORDS: Chiroptera, dental traits, oligodontia, phylogenetic comparative methods, polyodontia.
piercing, premolars and molars: chewing/grinding). Dietary specialization is considered one of the major evolutionary forces shaping the morphology of mammalian dentitions (Hunter and Jernvall 1995; Butler 2000), to the point that mammals that differ in diet also vary greatly in tooth number, size, and shape (Jernvall and Thesleff 2012), and some dental traits have evolved numerous times in association with particular diets (Hunter and Jernvall 1995). However, recent studies suggest that the relationship between dental morphology and diet is not always strong, with some changes in dental morphology being independent from changes in diet (e.g., Lister 2013). Together with experimental genomic evidence (Pallares et al. 2017), this highlights that diversity in mammalian dental phenotypes are also the product of other factors such as changes in life history strategies, developmental constraints, and phylogenetic effects (Gamarra et al. 2016; Monson and Hlusko 2018; Monson et al. 2019).

Dental variation within and among species of mammals also includes dental anomalies, which are relatively rare, generally found in few individuals or populations, and involve changes in the number, size, shape, and position of teeth (Miles and Grigson 2003). Mammalian dental anomalies can be categorized into two major types: oligodontia and polyodontia, which represent variations in the number of teeth (López-Aguirre 2014). While oligodontia implies the absence of specific teeth, the polyodontia, also called supernumerary teeth, hyperdontia, hypodontia, or polyodontism (Rodríguez and Cerviño 2009) implies the presence of additional teeth. The etiology of these conditions is controversial and different hypotheses have been proposed to explain them: (1) specific mutations in genes such as Msx1 and Pax9 (Line 2001); (2) isolated mutations in genes such as Sonic hedgehog (ssh), which is responsible for the normal development of molars and incisors (Dassule et al. 2000); (3) genetic changes during the tooth germ’s development, which generate a complete binary division in this structure (Wolsan 1984); (4) the appearance and subsequent development of an additional tooth germ, caused by physical damage, trauma, or genetic factors (Wolsan 1984); (5) embryological abnormalities (Anthonappa et al. 2013), and (6) changes in cell signaling (Kangas et al. 2004). Additionally, it has been suggested that dental anomalies can result from limited gene flow or environmental instability (Martin 2013; Chemisquy and Martin 2016).

Numerous cases of dental anomalies have been reported across mammal groups, including primates (Bateson 1892), Pilosa (McAfee 2014), rodents (Libardi and Percequillo 2014), marsupials (Martin and Chemisquy 2018), felids (Gomerčić et al. 2009), cervids (Azorit et al. 2002), pinnipeds (Loch et al. 2010), and bats (Rui and Drehmer 2004; Esquivel et al. 2017, 2020). Most studies to date have focused on describing the types and frequency of anomalies within populations, and/or been carried out at relatively small taxonomic scales (e.g., Drehmer et al. 2004; Martin 2007; Asahara et al. 2012; Esquivel et al. 2017). Only recently, the evolutionary patterns and implications of dental anomalies have begun to be explored in greater depth; these studies have suggested dental anomalies may provide clues to phylogenetic relationships and evolutionary mechanisms of morphological diversification (McAfee 2014; Drehmer et al. 2015; Jung et al. 2016). Despite these advances, the macroevolutionary patterns—including the phylogenetic signal and rates of evolution—of dental anomalies in species-rich mammal groups have received little attention, even though dental variability in general has been the subject of numerous studies (e.g., Grieco et al. 2013; Asahara et al. 2016). Investigating the interspecific variation of dental anomalies within phylogenetic and ecological contexts is fundamental for understanding the factors that potentially constrain or relax their frequency, and their potential importance as a source of dental diversity among species.

Because bats are the mammal group with the highest incidence of dental anomalies reported to date (López-Aguirre 2014) and they constitute a morphologically and ecologically diverse clade (Simmons 2005), we used them as a model system to answer the following questions: (1) Does phylogenetic relatedness predict the incidence of each type of dental anomaly across bats?; (2) Does the incidence of dental anomalies vary across different teeth according to their function?; and (3) Do specific diets constrain the incidence of dental anomalies? Because dental anomalies are thought to be the result of idiosyncratic mutations or random developmental disorders (Wolsan 1984; Nieminen 2013), we do not expect to find a phylogenetic signal for any type of dental anomaly. Because most bats rely on extensive mastication to process food items, we also predict that dental anomalies will affect molariform teeth (molars and premolars) to a lesser extent. Finally, because craniodental morphology and function are strongly linked to diet in bats (Freeman 1988, 1998; Freeman and Lemen 2010; Santana et al. 2011), we predict that specific dental anomalies will be shared among bats with similar dietary morphological specializations, including molar complexity and spatial constraints of the skull (e.g., rostrum contraction or elongation in frugivorous and nectarivorous bats, respectively). To test these predictions, we compiled a large dataset of dental anomalies in bats from the literature and museum specimens, and employed phylogenetic comparative methods to assess the macroevolutionary patterns of dental anomalies in Chiroptera.

**Material and Methods**

**DATA COLLECTION**

We compiled an extensive database of dental anomalies spanning 17,905 bat specimens using the following resources:
Scientific articles and specialized literature

We surveyed reports from the literature, including extensive reviews made by Phillips (1971), Lanza et al. (2008), and López-Aguirre (2014), and compiled publications from databases such as Google Scholar (https://scholar.google.com/), ISI Web of Knowledge (https://login.webofknowledge.com), Scopus (https://www.scopus.com/), Biodiversity Heritage Library (https://www.biodiversitylibrary.org/), and institutional repositories using the following keywords in Spanish, English, and Portuguese: “Bat” OR “Chiroptera,” AND “dental anomalies,” “abnormal,” “extra teeth,” “hyperdontia,” “oligodontia,” “polyodontia,” “supernumerary teeth,” “hypodontia,” and “dental variation.” We included published articles from 1910 until 2018 and excluded doubtful records such as commentaries or personal observations in this review. From each publication, we extracted the following information for our analysis: (I) type of dental anomaly reported (oligodontia or polyodontia), (II) number and type of affected teeth (incisors, premolars, or molars), (III) location of anomaly (upper or lower jaw), (IV) number of individuals with anomalies recorded by author(s), and (V) total number of individuals clearly reviewed by the author(s). Publications that did not provide sufficient data were not included. Additionally, we extracted data about total number of teeth from academic internet sites (e.g., Animal Diversity Web) and the literature (Gardner 2008; Mammal Species Accounts).

Scientific collections

We examined a total of 540 individuals from scientific collections, during 2017 and 2019, from the families Emballonuridae, Molossidae, Phyllostomidae, and Vespertilionidae. We focused on these groups because they are the largest and most diverse bat families, and commonly found in mammalian collections. Additionally, this effort was aimed at filling literature gaps by attempting to find new records of dental anomalies in species not previously known to show them. We examined specimens housed mainly in the Museo de Historia Natural Universidad de Los Andes, Bogotá-Colombia (Andes-M); Museo de Historia Natural Universidad Distrital Francisco José de Caldas, Bogotá-Colombia (MUD); Museo Javeriano de Historia Natural “Lorenzo Uribe, S.J.”, Bogotá-Colombia (MUJ); Museo de La Salle, Bogotá-Colombia (MLS-BOG); Museo Nacional do Rio de Janeiro, Rio de Janeiro-Brazil (MNRJ); and Museu de Zoologia da Universidade de Sao Paulo, Sao Paulo-Brazil (MZUSP). A complete list of museums housing the specimens examined, along with their catalogue numbers, can be found in Data S1.

For the purposes of this study, supernumerary teeth (polyodontia) was defined as extra teeth, each with an independent, partially or fully developed dental alveolus (Fig. 1), whereas oligodontia was defined as the absence of teeth in their normal position without traces of a developed dental alveolus where the tooth should have been. Thus, individuals with missing teeth that could have been lost during their life or as specimens were not included. Our dental nomenclature follows Miller (1907): upper incisors (I2-I3), upper premolars (P1-P2), upper molars (M1-M2-M3), lower incisors (i1-i3), lower premolar (p1-p3), and lower molars (m1-m3). This nomenclature was used for all bats with the exception of those within the family Pteropodidae, for which we followed Giannini and Simmons (2007). The taxonomic classification of Neotropical genera and species follows Gardner (2008) and Baker et al. (2016), whereas Old World species taxonomy follows Wilson and Mittermeier (2019). Using the literature and museum data, we calculated the relative frequency and percentage of each anomaly per bat family, genus, and species.

Dietary information was obtained from published sources. For all bat species considered in this study (N = 269), we first summarized quantitative and qualitative dietary information from the literature into six categories comprising the main food items identified in diets: carnivory (small vertebrates), frugivory (fruit), insectivory (arthropods), nectarivory (pollen and nectar), omnivory (fruits, insects, nectar and vertebrates), and sanguivory (blood). We then defined the following ranks based on the relative frequency of food items (1, occasional; 2, predominant; 3, strict), and assigned a rank to each dietary category for each species. Although this classification does not fully represent the variation of bat diets (e.g., dietary diversity is more complex and poorly documented for most bat species), previous studies have successfully used similar approaches to identify ecological drivers of...
Results

DENTAL ANOMALIES ACROSS BATS
From a review of 81 publications and 540 museum specimens, we found 834 individuals with dental anomalies among the 17,905 bats examined (4.65% estimated incidence in bats; Data S4). We recorded the presence of dental anomalies in seven families, 67 genera, and 128 species (Data S5). Phyllostomidae, Vespertilionidae, and Pteropodidae showed the highest incidence of anomalies; the genera *Myotis* (Vespertilionidae) and *Artibeus* (Phyllostomidae) had the greatest number of records, with 19 and 10 species exhibiting anomalies, respectively. *Myotis occultus* was the taxon with the highest number of anomalies (N = 96). The most common dental anomaly was oligodontia (N = 508; 60.9% of total anomalies), which also had the highest incidence in the total number of records of anomalies for Mormoopidae (87.0%), Vespertilionidae (79.3%), Pteropodidae (60.3%), and Phyllostomidae (56.7%). In sharp contrast, polyodontia (N = 326; 39.1%) was most frequent among Molossidae (90.0%) and Emballonuridae (73.7%). The frequency and teeth affected by anomalies differed among families. Molars did not exhibit anomalies in Emballonuridae, Molossidae, Mormoopidae, and Vespertilionidae, but anomalies were quite common in the molars of Phyllostomidae and Pteropodidae. The number of taxa with records of dental anomalies, the incidence by tooth-bearing bones (e.g., maxilla, mandible), and the frequency of oligodontia and polyodontia by family are shown in Table 1.

PHYLOGENETIC SIGNAL
We found a significant phylogenetic signal for dental anomalies combined (oligodontia and polyodontia) in bats (Blomberg’s K = 0.431, P < 0.001; Pagel’s λ = 0.845, 95% confidence interval [CI] = 0.53–0.99, P = 1.116 × 10⁻⁹, Fig. 2). When considered separately, we also found a significant phylogenetic signal for oligodontia (Blomberg’s K = 0.440, P < 0.009; Pagel’s λ = 0.252, 95% CI = 0.02–0.99, P = 0.045), and for polyodontia using K (Blomberg’s K = 0.429, P < 0.008) but not Pagel’s λ (λ = 0.553, 95% CI = 0.01–0.94, P = 0.063; Data S6).

ANOMALIES BY TOOTH TYPE
When we compared anomalies among different types of teeth, the premolars (N = 321) and molars (N = 295) appear to have the highest incidence of anomalies. Nonetheless, we did not find significant differences in the number of anomalies among tooth types (phylogenetic ANOVA: F = 0.032, P = 0.968). For all tooth types, oligodontia was the most common anomaly, with a greater incidence in the premolars (67.3%). Across the maxillary and mandibular toothrowss, the former exhibited significantly more anomalies in Vespertilionidae (88.3%), Emballonuridae (81.6%), and Molossidae (66.7%) compared to the other families in the sample (Table 1). Across all specimens, we did not find anomalies in the canines.

We did not find an association between the percentage incidence of dental anomalies and the total number of teeth, or the number of incisors, premolars, or molars, respectively. Nonphylogenetic correlations between the percentage of dental...
Table 1. Proportion of dental anomalies in major Chiroptera families, indicating the number of taxa affected, coverage by family, total specimens examined, incidence in maxilla and mandible, and anomaly type frequency. Rhinolophidae was not included due to scarce records.

| Family          | Genus | Coverage by family | Species | Total specimens examined | Most common teeth with anomaly | Incidence (%) | Frequency (%) |
|-----------------|-------|--------------------|---------|--------------------------|--------------------------------|---------------|--------------|
|                 |       |                    |         |                          | Maxilla | Mandible | Oligodontia | Polyodontia |
| Emballonuridae  | 4     | 28.6%               | 6       | 971                      | Incisors | 81.6     | 18.4        | 26.3        | 73.7        |
| Molossidae      | 5     | 23.8%               | 6       | 506                      | Premolars | 66.7     | 33.3        | 10.0        | 90.0        |
| Mormoopidae     | 2     | 100%                | 6       | 1026                     | Incisors | 56.5     | 43.5        | 87.0        | 13.0        |
| Phyllostomidae  | 28    | 46.7%               | 50      | 9807                     | Molars  | 43.8     | 56.2        | 56.7        | 43.3        |
| Pteropodidae    | 15    | 33.3%               | 24      | 2209                     | Premolars | 53.7    | 46.3        | 60.3        | 39.7        |
| Vespertilionida | 12    | 22.2%               | 35      | 3298                     | Molars  | 88.3    | 11.7        | 79.3        | 20.7        |

Figure 2. Bat phylogeny showing the percentage incidence of combined anomalies across families. Branches are colored according to ancestral state estimation using maximum likelihood.

ANOMALIES AND DIET

We found that dental anomalies tend to affect the same teeth according to dietary category. In insectivorous bats, the molars were not as affected by anomalies as the premolars (78.7%) and incisors (20.9%) considering the total dental anomalies within this group. Among frugivorous bats, oligodontia was the most common dental anomaly, mainly affecting both upper and lower molars (76.3%) and incisors (17.4%). In nectarivorous bats, oligodontia was the most common anomaly, mainly affecting the incisors (48.4%). Despite this apparent link between diet and the presence of certain dental anomalies affecting specific teeth, we found no significant relationship between dietary categories and the total incidence of combined dental anomalies (phylogenetic ANOVA $F_{5,197} = 0.88$, $R^2 = 0.022; P = 0.494; \lambda = 0.81$, 95% CI = 0.43–0.97), oligodontia ($F_{5,107} = 2.14$, $R^2 = 0.091; P = 0.066; \lambda = 0$, 95% CI = 0.0–0.53), or polyodontia ($F_{5,107} = 1.851$, $R^2 = 0.0796; P = 0.109; \lambda = 0$, 95% CI = 0.0–0.75; Fig. 3).

Discussion

We present the first phylogenetic comparative study of dental anomalies in bats, which allowed us to identify evolutionary trends and potential mechanisms that might contribute to the morphological diversity of an important component of the vertebrate feeding apparatus. In mammals and other vertebrates, evolutionary shifts in dentition range from the loss of a few teeth to the loss or gain of entire tooth classes. In this regard, our findings highlight the role of phylogenetic relatedness in driving these processes, and the need for quantitative phylogenetic analyses not...
only to better understand the dental evolution of these organisms, but to expand upon existing hypotheses about the possible links among tooth morphology, function, loss, and gain.

By examining a large and diverse sample of bat species, we found dental anomalies exhibit a significant phylogenetic signal, suggesting that their incidence is not only due to random mutations as previously considered, but also to processes tied to phylogenetic relatedness. We also found strong patterns in the types of dental anomalies among bat families; oligodontia has a greater incidence in the families Vespertilionidae, Mormoopidae, Phyllostomidae, and Pteropodidae, whereas polyodontia is most common in Molossidae and Emballonuridae. Overall, the frequency of dental anomalies in Chiroptera (4.65%) is lower than that described for other mammalian taxa to date (e.g., Pongidae 5.2%, Miles and Grigson 2003; Otaria 12.1%, Drehmer et al. 2004; Ursus cinereoargenteus 34.7% and Vulpes vulpes 16.6%, Gisburne and Feldhamer 2005; Talpa altaica 22.9%, Kawada et al. 2006; Didelphis albiventris 8.14%, Chemisquy and Martin 2016, among others). Our data also suggest that bats show no evidence of a specific sexual bias or population/geographic pattern in their dental anomalies.

Previous studies in other mammal groups proposed that dental anomalies are associated with reversal events (i.e., evolutionary throwbacks or atavism; Hall 2010), inbreeding and limited gene flow (Martin 2013), environmental instability (Chemisquy and Martin 2016), and fluctuating asymmetry or random mutations (Hauer 2002), among other factors. Here, using a large and diverse dataset and modern phylogenetic tools, we showed that phylogenetic relatedness is likely a more relevant factor driving the macroevolutionary patterns of dental anomalies across bat lineages. This finding may imply latent and historical explanations for the incidence of dental anomalies, which may or may not be explored by current hypotheses that focus on environmental or developmental instability. Our results thereby highlight the potential importance of less known processes that could be sources of dental diversity, including evolutionary trends toward reduction, loss, or gain of teeth.

Under an adaptive scenario, the performance of anatomical structures that are critical to survival is expected to be under selection; therefore, teeth that have a more important function during feeding should exhibit a lower incidence of anomalies if these decrease feeding performance. Nevertheless, although most bats predominantly use their molariform dentition during feeding (Santana and Dumont 2009; Santana et al. 2010, 2011), we found that these teeth are highly affected by anomalies. Trends associated with diet provide further insight into this unexpected finding; although we did not find a significant relationship between dental anomalies and diet categories across bats, the proportion of anomalies in molariform teeth differs between frugivorous and insectivorous bats. Frugivorous bats exhibit a higher incidence of anomalies in their molars, whereas insectivores have a greater incidence of anomalies in their premolars and lacked anomalies in their molars. This could indicate a certain level of functional constraint on the incidence of anomalies in the molars of insectivorous bats, which masticate insect prey thoroughly (Santana et al. 2011), or that dilambdodont molars (with W-shaped cusps,
Changes in dental patterns may reflect micro- and macroevolutionary processes that influence dental diversification (Line 2003), and may have played a key role in the ecological diversification of bat families. However, genetic drift may also be an important factor in the incidence of dental anomalies (Asahara et al. 2012); smaller populations are more prone to genetic drift and consequently would have a higher probability of mutations that would result in dental anomalies (Asahara et al. 2012). Consistent with this idea, it has been reported that the frequency of dental anomalies is greater in marginal populations of small mammals (e.g. Tulpa daviviana, Scapanus latimanus, and Mogera wogura) and that this process might substantiate changes in their dental formula (Hall 1940; Kawada et al. 2011; Asahara et al. 2012).

All data reported here and used in our analysis come from specimens housed in natural history collections. This may pose two potential sources of bias in our analysis. First, there is generally a bias in collections to overrepresent the most abundant species and underrepresent the rare species, which can affect their estimated incidence of dental anomalies. Although we tried to balance the different taxa in our study (Data S7A), this was ultimately an issue beyond our control. However, we found that the major trends described here—including the high phylogenetic signal of dental anomalies—still hold when different samples sizes are analyzed (Data S7B). Second, the possible existence of taxonomic errors in the dataset could also affect our results; although the 540 specimens reviewed by us were carefully identified following the most up-to-date taxonomy, data from the literature could include some misidentified specimens. We tried to mitigate this source of error by including only indexed articles described by taxonomic specialists, or in which the taxonomic identification process was clearly described. Additionally, we updated the taxonomy of all the species considered in this study, so that we did not include old names or synonyms.

Conversely, our results also have implications for taxonomy. Ignoring dental anomalies and their link with phylogenetic relatedness can lead to taxonomic misidentification and errors, including the description of new invalid or endemic species, or new distributional records (Lanza et al. 2008; Martínez-Arias et al. 2010). Although not an unknown problem by taxonomists, dental anomalies have gone largely unnoticed. Our results demonstrate that the number of bat species with dental anomalies has been highly underestimated. In the last review of the topic, López-Aguirre (2014) recorded six families, 36 genera, and 64 species with dental anomalies, whereas we report twice this number of species. Finally, dental anomalies appear to occur to a greater extent in groups with complex taxonomic histories and whose dental characters are indispensable for correct identification (e.g., Glossophaginæ, Stenodermatinæ, and Vespertilionidæ, among others). Therefore, understanding the patterns and incidence of dental anomalies and their variations across clades is fundamental for future taxonomic studies in bats and other small mammals.
As mammalian dental formulas are often considered to be fixed phenotypes, dental anomalies provide a system in which it would be particularly interesting to explore the links among phylogeny, development, ecology, and morphological change. The radiation of mammals, its high morphological and ecological diversity, and the increasing availability of modern phylogenetic and genomic tools will likely allow future studies uncover unknown micro- and macroevolutionary processes underlying the patterns in dental anomalies described here. Our results present a significant contribution to broader efforts aimed at understanding the evolution of dental diversity in mammals. Ultimately, we expect that the results presented here will also provide a useful starting point toward other studies that analyze the incidence and evolutionary patterns of anatomical anomalies, and their potential implications for morphological diversification.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
DAE designed the study. All authors contributed to the analytical design, interpretation of the results, and writing the manuscript and gave approval for publication.

ACKNOWLEDGMENTS
We thank S. Solari and G. S. T. Garbino, who provided useful comments and many suggestions that helped improve an early version of the manuscript. DAE thanks to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) – Finance Code 88882.439397/2019-01 (Master Degree) and RM thanks to CAPES, CNPq, and UFRGS for financial support.

DATA ARCHIVING
All data associated with this study are archived in the Supporting Information of this article and available under CC0 on Dryad: https://doi.org/10.5061/dryad.zcrjdfn9x

LITERATURE CITED
Anthonappa, R. P., N. M. King, and A. B. Rabie. 2013. Aetiology of supernumerary teeth: a literature review. Eur. J. Paediatr. Dent. 14:279–288.
Asahara, M., A. Kryukov, and M. Motokawa. 2012. Dental anomalies in the Japanese mole Mogera wogura from northeast China and the Primorsky region of Russia. Acta Theriol. 57:41–48.
Asahara, M., K. Saito, T. Kishida, K. Takahashi, and K. Bessho. 2016. Unique pattern of dietary adaptation in the dentition of Carnivora: its advantage and developmental origin. Proc. R. Soc. B 283:20160375.
Azorit, C., J. Muñoz-cobo, and M. Analla. 2002. Abnormal teeth in the Spanish red deer Cervus elaphus hispanicus. Z. Jagdwiss. 48:252–260.
Baker, R. J., S. Solari, A. Cirranello, and N. B. Simmons. 2016. Higher level classification of phyllostomid bats with a summary of DNA synapomorphies. Acta Chiropt. 18:1–38.
Bateson, W. 1892. On numerical variation in teeth, with a discussion of the patterns of dental anomalies. Proc. R. Soc. B 283:20160375.
Bergqvist, L. P. 2003. The role of teeth in mammal history. Braz. J. Oral. Sci. 2:249–257.
Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.
Butler, P. M. 2000. The evolution of tooth shape and tooth function in pri-mates. Pp. 201–211 in M. F. Teaford, M. M. Smith, and M. W. Ferguson, eds. Development, function, and evolution of teeth. Cambridge Univ. Press, Cambridge, U.K.
Chemisquy, M. A., and G. M. Martin. 2016. Dental anomalies in Didelphis albiventris (Mammalia, Marsupialia, Didelphidae) from Argentina, Brazil and Uruguay. Beringia Ser. Zool. 106:e2016023.
Churchill, M., and M. T. Clementz. 2015. Functional implications of variation in tooth spacing and crown size in Pinnipedia (Mammalia: Carnivora). Anat. Rec. 298:878–902.
Clemens, W. A. 1970. Mesozoic mammalian evolution. Annu. Rev. Ecol. Syst. 1:357–390.
Dassule, H. R., P. Lewis, M. Bei, R. Maas, and A. P. McMahon. 2000. Sonic hedgehog regulates growth and morphogenesis of the tooth. Development 127:4775–4785.
Cocos, A., and D. J. Halazonetz. 2017. Craniofacial shape differs in patients with tooth agenesis: geometric morphometric analysis. Eur. J. Orthod. 39:345–351.
Dumont, E. R., K. Samadovam, I. Grosse, O. M. Warsi, B. Baird, and L. M. Dávalos. 2014. Selection for mechanical advantage underlies multiple cranial optima in New World leaf-nosed bats. Evolution 68:1436–1449.
Dreher, C. J., M. E. Fabian, and J. O. Meneghetti. 2004. Dental anomalies in the Atlantic population of South American sea lion, Otaria byronia (Pinnipedia, Otariidae): evolutionary implications and ecological approach. Lat. Am. J. Aquat. Mamm. 3:7–18.
Dreher, C. J., D. Sanfelice, and C. Loch. 2015. Dental anomalies in pinnipeds (Carnivora: Otariidae and Phocidae): occurrence and evolutionary implications. Zoomorphology 134:325–338.
Esquivel, D. A., D. Camelo-Pinzón, and A. Rodríguez-Bolaños. 2017. New record of bilateral hyperdontia in Carollia brevicauda (Chiroptera: Phyllostomidae). Theria 8:71–73.
Esquivel, D. A., C. Aya-Cuero, A. P. Penagos, J. Chacón-Pacheco, C. J. Agámez-López, A. V. Ochoa, H. E. Ramírez-Chaves, and D. Bennett. 2020. Updating the distribution of Vampyrum spectrum (Chiroptera, Phyllostomidae) in Colombia: new localities, potential distribution and notes on its conservation. Neotrop. Biol. Conserv. 15:689–709.
Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. Am. Nat. 160:712–726.
Freeman, P. W. 1988. Frugivorous and animalivorous bats (Microchiroptera) - dental and cranial adaptations. Biol. J. Linn. Soc. 33:249–272.
———. 1998. Form, function, and evolution in skulls and teeth of bats. Pp. 140–156 in T. H. Kunz and P. A. Racey, eds. Bat biology and conservation. Smithsonian Institution Press, Washington, D.C.
Freeman, P. W., and C. Lemen. 2010. Simple predictors of bite force in bats: the good, the better and the better still. J. Zool. 275:477–486.
Freeman, P. W., and C. Lemen. 2010. Simple predictors of bite force in bats: the good, the better and the better still. J. Zool. 275:477–486.
Gamarra, B., M. N. Delgado, A. Romero, J. Galbany, and A. Pérez-Pérez. 2016. Phylogenetic signal in molar dental shape of extant and fossil catarrhine primates. J. Hum. Evol. 94:13–27.
Gardner, A. L. 2008. Mammals of South America. Volume 1: marsupials, xenarthrans, shrews, and bats. Univ. of Chicago Press, Chicago.
Giannini, N. P., and N. B. Simmons. 2007. Element homology and the evolution of tooth spacing and crown size in Pinnipedia (Carnivora). Acta Theriol. 57:717–745.
Gisburne, T. J., and G. A. Feldhammer. 2005. Dental anomalies in the gray fox Urocyon cinereoargenteus and the red fox Vulpes vulpes. Acta Theriol. 50:515–520.
DENTAL ANOMALIES IN BATS

Luo, Z. X., R. L. Cifelli, and Z. Kielan-Jaworowska. 2001. Dual origin of tribosphenic mammals. Nature 409:53–57.

Marroig, G., and J. M. Cheverud. 2005. Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in New World monkeys. Evolution 59:1128–1142.

Martin, G. M. 2007. Dental anomalies in Dromiciops glioides (Microbiotheria, Microbiotheriidae), Caenolestes fuliginosus and Rhyncholestes raphanus (Pacuicteculata, Caenolestidae). Rev. Chil. Hist. Nat. 80:393–406.

———. 2013. Intraspecific variability in Lestoros inca (Pacuicteculata, Caenolestidae), with reports on dental anomalies and eruption pattern. J. Mammal. 94:601–617.

Martin, G. M., and M. A. Chemisquy. 2018. Dental anomalies in Caluromys (Marsupialia, Didelphimorphia, Didelphidae, Caluromyinae) and a reassessment of malformations in New World marsupials (Didelphimorpha, Microbiotheriia and Pacuicteculata). Mammalia 82:500–508.

Martínez-Arias, V. M., S. Solari, and J. F. Díaz-N. 2010. Re-evaluation of a Colombian record of Sturiria thomasi de La Torre and Schwartz, 1966 (Phylllostomatidae: Stenodermatinae). Chiropt. Neotrop. 16:603–609.

McAfee, R. K. 2014. Dental anomalies within extant members of the mammalian Order Pilosa. Acta Zool. 96:301–311.

Miles, A. E. W., and C. Grigson. 2003. Colyer’s variations and diseases of the teeth of animals. Cambridge Univ. Press, London, U.K.

Miller, G. S., Jr. 1907. The families and genera of bats. Bull. U.S. Natl. Mus. 57:1–282.

Monson, T. A., and L. J. Hlsuco. 2018. Breaking the rules: phylogeny, not life history, explains dental eruption sequence in primates. Am. J. Phys. Anthropol. 167:217–233.

Monson, T. A., J. L. Coleman, and L. J. Hlusko. 2019. Craniodental allometry, prenatal growth rates, and the evolutionary loss of the third molars in New World monkeys. Anat. Rec. 302:1419–1433.

Nanova, O. G. 2015. Morphological variation and integration of dentition in the Arctic fox (Vulpes lagopus): effects of island isolation. Russ. J. Theriol. 14:153–162.

Niemenin, P. 2013. Dental anomalies: genetics. CLS 1–15.

Oeschger, E. S., G. Kanavakis, D. J. Halazonetis, and N. Gkantidis. 2020. Number of teeth is associated with facial size in humans. Sci. Rep. 10:1–7.

Orme, D., R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, and W. Pearse. 2018. Raper: comparative analyses of phylogenetics and evolution in R. R package version 1.0.1. Available via https://CRAN.R-project.org/package=raper.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Pallares, L. F., R. Ledevin, S. Pantalacci, L. M. Turner, E. Steingrimsson, and S. Renaud. 2017. Genomic regions controlling shape variation in the first upper molar of the house mouse. Elite f.e:29510.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Phillips, C. J. 1971. The dentition of glossophaginae bats: development, morphological characteristics, variation, pathology, and evolution. Univ. of Kansas Press, Lawrence, KS.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available via http://www.R-project.org/.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3:217–223.

Rodríguez, F. J., and S. Cerviño. 2009. Múltiples dientes supernumerarios distomolares. Av. Odontostomatol. 25:319–325.
Rui, A. M., and C. J. Drehmer. 2004. Anomalies and variation in the dental formula of bats of the genus *Artibeus* Leach (Chiroptera, Phyllostomidae). Rev. Bras. Zool. 21:639–648.

Santana, S. E., and E. R. Dumont. 2009. Connecting behaviour and performance: the evolution of biting behaviour and bite performance in bats. J. Evol. Biol. 22:2131–2145.

Santana, S. E., E. R. Dumont, and J. L. Davis. 2010. Mechanics of bite force production and its relationship to diet in bats. Funct. Ecol. 24:776–784.

Santana, S. E., S. Strait, and E. R. Dumont. 2011. The better to eat you with: functional correlates of tooth structure in bats. Funct. Ecol. 25:839–847.

Shi, J. J., and D. L. Rabosky. 2015. Speciation dynamics during the global radiation of extant bats. Evolution 69:1528–1545.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529 in D. E. Wilson and D. M. Reeder, eds. Mammal species of the World: a taxonomic and geographic reference. Johns Hopkins Univ. Press, Baltimore, MD.

Slaughter, B. H. 1970. Evolutionary trends of chiropteran dentitions. Pp. 50–83 in B. H. Slaughter and D. W. Walton, eds. About bats. Southern Methodist Univ. Press, Dallas, TX.

Wainwright, P. C. 2007. Functional versus morphological diversity in macroevolution. Annu. Rev. Ecol. Evol. Syst 38:381–401.

Wilson, D. E., and R. A. Mittermeier. 2019. Handbook of the mammals of the world. Vol. 9. Bats. Lynx Edicions, Barcelona, Spain.

Wolsan, M. 1984. The origin of extra teeth in mammals. Acta Theriol. 29:128–133.

**Associate Editor: T. Ezard**

**Handling Editor: A.G. McAdam**

---

**Supporting Information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Supplementary Data 1.** Number of specimens included per species of bats, and the list of museums and catalogue numbers of specimens examined.

**Supplementary Data 2.** Dietary classification for 269 bat species used in the present study.

**Supplementary Data 3.** Phylogeny of 269 bat operational taxonomic units (OTUs) with dental anomalies data.

**Supplementary Data 4.** Bat family, species, type of anomaly, number of individuals with anomalies, total number recorded, and percentage incidence analyzed in this study.

**Supplementary Data 5.** Bat families, genus and species recorded with dental anomalies.

**Supplementary Data 6.** Phylogenies showing the percentage incidence of dental anomalies in oligodontia (left), and polyodontia (right) across species, with branch colors representing ancestral state estimation using maximum likelihood.

**Supplementary Data 7A.** Bar plots showing the extent of the data coverage. The first bar plot shows raw data and the second log raw data. **7B.** Estimating the effect of sample size.