

Evolutionary implications of dental anomalies in bats

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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.

A major goal in evolutionary biology is to understand the mechanisms that underlie phenotypic diversity. Variation in phenotypic traits can be the product of natural selection (e.g., through pressures exerted by environmental factors and/or biotic interactions), stochastic processes (genetic drift), evolutionary history (phylogenetic relatedness), or developmental and physiological constraints, among other processes (Marroig and Cheverud 2005; Wainwright 2007; Losos 2011). Within this framework, a major and productive area of study has been to explore the degree to which novel morphologies may ultimately lead to adaptive macroevolutionary changes (Jernvall and Thesleff 2012). In this

regard, an issue that has regained attention in recent years is the role of dental alterations or anomalies and their possible contribution to phenotypic novelty in the adaptation to new feeding niches in mammals and other vertebrates (Churchill and Clements 2015; Drehmer et al. 2015; Nanova 2015; Asahara et al. 2016; Kahle et al. 2018).

The evolution of a heterodont dentition in the late Triassic was a key innovation that contributed to the evolutionary success of mammals (Clemens 1970; Butler 2000; Luo et al. 2001; Bergqvist 2003). This dentition is characterized by four tooth types, each with a specialized function (incisors: cutting, canines:

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, hyperdoncia, hyperdontia, or polydontism (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* (*shh*), 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); Museu Nacional do Rio de Janeiro, Rio de Janeiro-Brazil (MNRJ); and Museu de Zoologia da Universidade de São Paulo, São 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

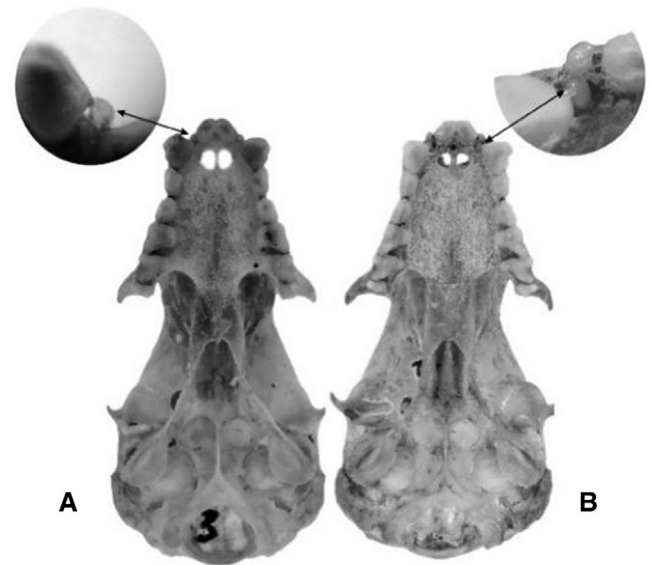


Figure 1. Example of polyodontia: (A) Ventral view of the cranium detailing the typical second incisors in *Carollia brevicauda* (Phyllostomidae) and (B) ventral view of the skull with extra incisors.

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

craniodental diversity in bats (e.g., Santana et al. 2010, 2011, Dumont et al. 2014). The dataset with the dietary information for the 269 bat species included in these analyses can be found in Data S2.

PHYLOGENETIC COMPARATIVE ANALYSES

We used a pruned version of one of the most comprehensively sampled, multilocus, species-level phylogenies for Chiroptera published by Shi and Rabosky (2015) for our comparative analyses. This tree was estimated using maximum likelihood from a supermatrix of mitochondrial and nuclear sequence data of 812 bat species and fossil calibrations. The phylogeny used, pruned for the species with dental anomaly data in this study, contained 269 species; the distribution of major clades along the phylogenetic tree used is depicted in Data S3.

To investigate the strength of phylogenetic signal in the percentage incidence of dental anomalies, we calculated Blomberg's K and Pagel's λ (Pagel 1999; Blomberg et al. 2003) for each type of dental anomaly. For Blomberg's K , a value of $K > 1$ indicates a stronger phylogenetic signal than expected under Brownian motion (BM); a value of 1 suggests variation along the phylogeny following BM; and a value < 1 suggests variation along the phylogeny is more random than expected under BM (Blomberg et al. 2003). Similarly, for Pagel's λ , a value of 1 suggests variation along the phylogeny following BM, whereas values closer to 0 indicate the opposite (Pagel 1999).

To investigate the relationship between dental anomalies and diet categories, we conducted phylogenetic ANOVAs (i.e., Phylogenetic Generalized Least Squares models) (Grafen 1989) using the percentage incidence of anomalies (both combined anomalies and for each anomaly type) per species as dependent variable, and ranked dietary categories as factors. The phylogenetic covariance matrix used in these analyses was weighted by Pagel's λ (Pagel 1999), which was estimated using maximum likelihood (Freckleton et al. 2002). Phylogenetic signal calculation and phylogenetic ANOVAs were performed using functions in the packages *ape* (Paradis et al. 2004), *geiger* (Harmon et al. 2008), *caper* (Orme et al. 2018), and *phytools* (Revell 2012) in R version 3.6.2 (R Core Team 2019). To visualize anomaly variation across the phylogeny, we mapped the percentage incidence of anomalies and estimated ancestral states using maximum likelihood with the *contMap* function in *phytools* (Revell 2012).

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 $\lambda = 0.845$, 95% confidence interval [CI] = 0.53–0.99, $P = 1.116 \times 10^{-9}$, Fig. 2). When considered separately, we also found a significant phylogenetic signal for oligodontia (Blomberg's $K = 0.440$, $P < 0.009$; Pagel's $\lambda = 0.252$, 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 ($\lambda = 0.553$, 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 tooththrows, 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	Molars	53.7	46.3	60.3	39.7
Vespertilionidae	12	22.2%	35	3298	Premolars	88.3	11.7	79.3	20.7

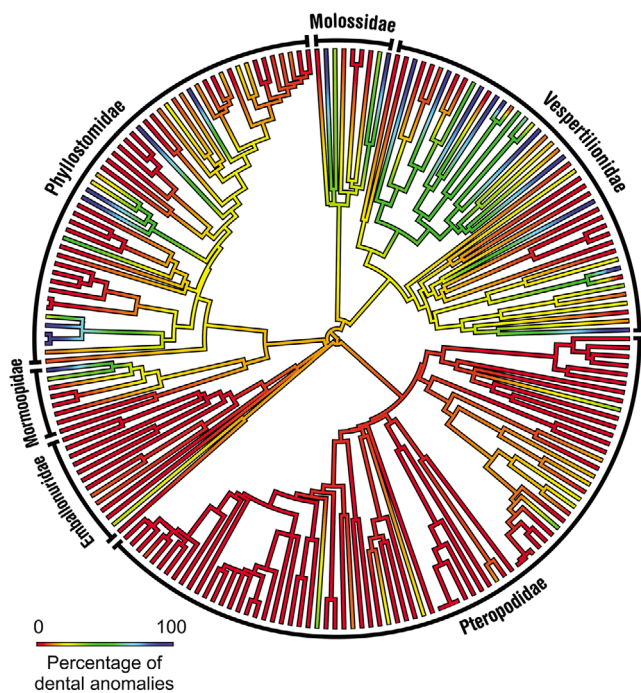


Figure 2. Bat phylogeny showing the percentage incidence of combined anomalies across families. Branches are colored according to ancestral state estimation using maximum likelihood.

anomalies and total number of teeth ($S = 4352$, $R = 0.125$, $P = 0.134$), number of incisors ($S = 4484$, $R = 0.098$, $P = 0.238$), number of premolars ($S = 4916$, $R = 0.012$, $P = 0.886$), and number of molars ($S = 4261$, $R = 0.143$, $P = 0.085$) per species were not significant ($P > 0.05$) using Spearman correlation. We found the same, nonsignificant trends when we incorporated the phylogeny using PGLS models with Lambda estimation (number of teeth: $R^2 = 0$, $P = 0.347$; number of incisors: $R^2 = -0.007$,

$P = 0.986$; number of premolars: $R^2 = -0.003$, $P = 0.478$; and number of molars: $R^2 = 0.001$, $P = 0.284$).

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

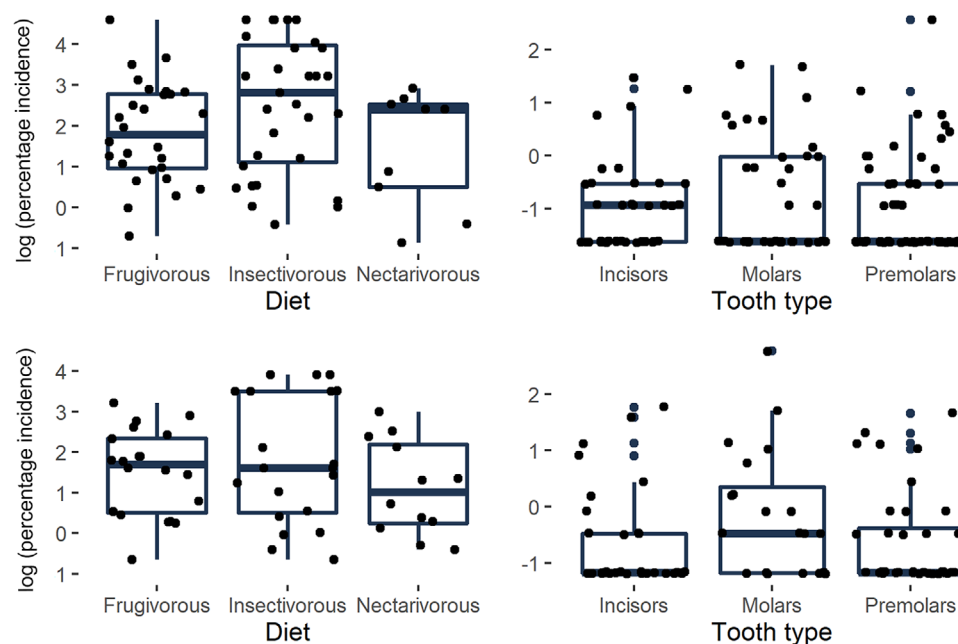


Figure 3. Boxplots showing the frequency of anomalies per diet category and tooth type with respect to oligodontia (upper line) and polyodontia (lower line).

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; *Urocyon 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,

typical of insectivorous mammals) are less subject to anomalous development. Indeed, molars with a more complex topography appeared to be less affected by anomalies. In frugivorous and nectarivorous bats, most molar anomalies involved the last molar in either the maxilla or the mandible. When present in bats, these teeth are highly variable in size and shape, and have a simpler cusp pattern when compared to anterior molars, which have a higher complexity (Santana et al. 2011). This suggests that, among the molariform teeth, those with lower dental complexity are more prone to dental anomalies and therefore to reduction and loss. Previous research has demonstrated that some dental traits are genetically independent from one another in mammals (Hlusko et al. 2011), and that molars and premolars represent two distinct genetic modules that are influenced by different degrees of pleiotropy (Grieco et al. 2013). Therefore, we hypothesize that these results may also be explained by genetic modularity in dental development. This mechanism could also explain the greater number of anomalies found in the maxillary versus the mandibular dental row.

Using dietary categories as proxies for craniodental specialization, we did not find support for our prediction that the morphological characteristics and spatial constraints of the skull may be linked with the incidence of dental anomalies in bats. Although we expected that clades with longer skulls (nectarivores) would be more likely to add teeth, and that shortened skulls (e.g., frugivores) would be more apt to experience tooth loss, our results did not support this prediction. For example, nectarivorous bats showed both polyodontia and oligodontia in all teeth without a specific pattern. Additionally, we did not find any relationship between the percentage incidence of dental anomalies and the total number of teeth, or the number of incisors, premolars, and molars, respectively. A complementary question is whether dental anomalies could have an impact on the facial morphology of bats instead. The relationship between oligodontia and craniofacial morphology has been well explored in humans, with recent studies revealing a connection between the two (Cocos and Halazonetis 2017). For example, Oeschger et al. (2020) found that women and men with missing teeth had, respectively, 0.59% and 0.56% smaller craniofacial configurations. Thus, individuals with anomalies may develop slightly longer or shorter faces to accommodate the supernumerary or lost teeth. Individual variation may also underpin other aspects of dental evolution (Asahara et al. 2012). For example, as tooth reduction in some families (e.g., Vespertilionidae, high premolar oligodontia) is usually accompanied by changes in the arrangement of premolar cusps or shelves, this could be a source for adaptation to new feeding niches via changes in the dental formulae if mastication of dietary items is improved (Slaughter 1970).

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., *Talpa 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., Glossophaginae, Stenodermatinae, and Vespertilionidae, 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 mammal 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.

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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>

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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.