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## Dietary and body-mass reconstruction of the Miocene neotropical bat *Notonycteris magdalenensis* (Phyllostomidae) from La Venta, Colombia

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**Abstract.**—With 14 species recorded, the Miocene La Venta bat fauna is the most diverse bat paleocommunity in South America. It includes the oldest plant-visiting bat in the New World and some of the earliest representatives of the extant families Phyllostomidae, Thyropteridae, and Noctilionidae. La Venta's *Notonycteris magdalenensis* is an extinct member of the subfamily Phyllostominae, a group of modern Neotropical animalivorous bats, and is commonly included in studies of the evolution of Neotropical bats, but aspects of its biology remain unclear. In this study, we used multivariate dental topography analysis (DTA) to reconstruct the diet of *N. magdalenensis* by quantitatively comparing measures of molar complexity with those of 25 modern noctilionoid species representing all major dietary habits in bats. We found clear differences in molar complexity between dietary guilds, indicating that DTA is potentially an informative tool to study bat ecomorphology. Our results suggest *N. magdalenensis* was probably an omnivore or insectivore, rather than a carnivore like its modern relatives *Chrotopterus auritus* and *Vampyrum spectrum*. Also, we reconstructed the body mass of *N. magdalenensis* to be ~95 g, larger than most insectivorous bats, but smaller than the largest carnivorous bat (*V. spectrum*). Our results confirm that *N. magdalenensis* was not a specialized carnivore. It remains to be demonstrated that the specialized carnivory ecological niche was occupied by the same lineage of phyllostomines from at least the middle Miocene. Combining our diet and body-mass reconstructions, we suggest that *N. magdalenensis* exhibits morphological pre-adaptations crucial for the evolution of specialized carnivory.

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### Introduction

With more than 200 living species, Phyllostomidae is the family with the highest ecomorphological diversity in the order Chiroptera. The range of dietary niches that phyllostomid bats occupy is unparalleled across Mammalia (Fleming 1986; Aguirre et al. 2003; Dumont et al. 2012; Santana et al. 2012; Arbour et al. 2019). Studies have classified noctilionoid bats into seven dietary guilds: carnivory, frugivory, insectivory, nectarivory, omnivory, piscivory, and sanguivory, with insectivory being the

most common (Norberg and Rayner 1987; Dumont et al. 2012; Santana et al. 2012; Denzinger and Schnitzler 2013). Reconstructions of dietary evolution in Phyllostomidae suggest that carnivory and nectarivory evolved independently multiple times in different lineages, diverging from an insectivorous common ancestor (Gunnell and Simmons 2005; Datzmann et al. 2010; Rojas et al. 2012; Santana and Cheung 2016; Davies et al. 2020). Morphological variability associated with diet-based functional demands is thought to have facilitated the ecological radiation and taxonomic

diversification in Phyllostomidae (Santana et al. 2012; Shi and Rabosky 2015; Arbour et al. 2019; Morales et al. 2019; Rossoni et al. 2019; Giannini et al. 2020; Hedrick et al. 2020). Traditionally, most studies on dietary ecomorphology in bats have focused on skull morphology to study the form–function link, providing crucial information to understand the range of morphological specializations (Aguirre et al. 2002; Monteiro and Nogueira 2011; Santana and Cheung 2016; Santana and Portugal 2016; Arbour et al. 2019; Rossoni et al. 2019). Some studies have also provided insights on the role of diet in the diversification of the postcranial skeleton (Vaughan 1959; Norberg and Rayner 1987; Louzada et al. 2019; Gaudioso et al. 2020; López-Aguirre et al. 2021) and external sensory organs (Brokaw and Smotherman 2020; Leiser-Miller and Santana 2020).

Despite the increasing evidence in support of diet as a key driver of bat evolution, reconstructing the macroevolutionary trajectories of dietary specializations in bats has been limited by the fossil record (Teeling et al. 2005). Compared with other tetrapod groups, the fossil record of Chiroptera has one of the lowest levels of taxonomic diversity and skeletal preservation, with an estimated 80% of the record missing (Eiting and Gunnell 2009; Brown et al. 2019). Geographic patterns in the completeness of the bat fossil record indicate that the Southern Hemisphere and Asia are especially underrepresented, obscuring important spatiotemporal information (Brown et al. 2019). In the Southern Hemisphere, two fossiliferous localities stand out in terms of bat fossil diversity: Riversleigh from the Oligocene to Pleistocene (ca. 25–2 Ma) of Australia with more than 40 species (Hand and Archer 2005), and La Venta from the middle Miocene (ca. 13–12 Ma) of Colombia with at least 14 species (Czaplewski et al. 2003).

The La Venta fossil fauna, recovered from the Villavieja Formation in Colombia's Huila Department, is the richest Cenozoic vertebrate fossil community of northern South America (83 fossil mammal species) (Kay and Madden 1997; Croft 2016). The deposits span a poorly represented period in the middle Miocene, and its fossil mammals have helped define the Laventan South American Land Mammal Age

(Madden et al. 1997). The La Venta bat community includes representatives of six families, including extinct representatives of the family Phyllostomidae (*Notonycteris magdalenensis*, *Notonycteris sucharadeus*, *Palynephyllum antimaster*), and the oldest evidence of modern species of families Noctilionidae (*Noctilio albiventris*) and Thyropteridae (*Thyroptera lavalii*) (Czaplewski 1997; Czaplewski et al. 2003). *Palynephyllum antimaster* represents the earliest phytophagous bat in the New World, a dietary strategy that provided a key evolutionary innovation for the order (Czaplewski et al. 2003; Yohe et al. 2015).

La Venta's *N. magdalenensis* is known from a dentary fragment containing a complete m1 and the anterior portion of m2, as well as several other isolated teeth (Savage 1951; Czaplewski 1997). Postcranial remains referred to this species include distal and proximal humeral fragments (Savage 1951; Czaplewski 1997; Czaplewski et al. 2003). When Savage (1951) described the species, he placed *N. magdalenensis* in the phyllostomid subfamily Phyllostominae, a group of Neotropical animalivorous and omnivorous bats. Subsequent phylogenetic analyses have upheld that placement and grouped it consistently in a clade with *Vampyrum spectrum* and *Chrotopterus auritus*, both large-bodied carnivorous species (Czaplewski et al. 2003; Dávalos et al. 2014). Comparisons of dental features and body size indicate that *N. magdalenensis* was larger than *C. auritus* but smaller than *V. spectrum*, the largest bat in the New World. This fossil species is often included in phylogenetic analyses, as a calibration point for dated phylogenies of the bat superfamily Noctilionoidea (Rojas et al. 2012; Dávalos et al. 2014; Hand et al. 2018). It also features in studies focused on the ecological history of phyllostomids, including the adoption of specialized ecological niches such as carnivory by the middle Miocene (e.g., Baker et al. 2012; Yohe et al. 2015; Simmons et al. 2020). Yet, despite its importance for the study of the evolution of Neotropical bats, studies focused on reconstructing the biology of *N. magdalenensis* are still needed.

Mammal teeth show highly specialized structures that vary in relation not only to

phylogeny but also to dietary differences, providing informative and widely used proxies to identify niche partitioning and reconstruct diets of extinct taxa, including bats (e.g., Czaplewski et al. 2003; Simmons et al. 2008, 2020; Self 2015; Hand et al. 2016). Studies of the dentition of *N. magdalenensis* by Savage (1951) and Czaplewski et al. (2003) concluded it lacks the highly specialized dental traits observed in its living carnivorous relatives *V. spectrum* and *C. auritus* (Freeman 1988, 1998), suggesting that *N. magdalenensis* probably had a less carnivorous diet. These dental features in *N. magdalenensis*, compared with those of its living carnivorous relatives, include relatively lower crown height, more robust crests and cusps, less reduced talonids in lower molars, less obliquely oriented ectoloph crests, and shorter postmetacrista in upper molars.

Dental topography analysis (DTA) is an informative quantitative approach to study dental morphology within an ecological context and has the potential to be incorporated into modern phylogenetic comparative methods (Evans et al. 2007; Bunn and Ungar 2009; Cooke 2011; Allen et al. 2015; Prufrock et al. 2016a; Pineda-Munoz et al. 2017; López-Torres et al. 2018; Selig et al. 2020). A battery of DTA metrics have been developed in recent decades (Evans et al. 2007; Boyer 2008; Bunn et al. 2011; Berthaume et al. 2019a), further developing the capacity to apply multivariate analyses (Pineda-Munoz et al. 2017). DTA has been widely used to study dietary adaptations in mammals (Lazzari et al. 2008; Selig et al. 2019, 2020), especially in primates (Ungar 2004; Bunn and Ungar 2009; Ledogar et al. 2013; Winchester et al. 2014; Allen et al. 2015; López-Torres et al. 2018; Ungar et al. 2018; Berthaume et al. 2020), and to analyze morpho-functional specializations (Bunn and Ungar 2009; Bunn et al. 2011), elucidate macroevolutionary trajectories (López-Torres et al. 2018), resolve systematic arrangements (Selig et al. 2020), and reconstruct ecological interactions (Prufrock et al. 2016a) across mammalian taxa. In bats, Santana et al. (2011) used DTA to explore diet-based adaptations in the occlusal surface of molars in Phyllostomidae, correlating plant-based diets with higher dental complexity.

We used 3D computational modeling, multivariate DTA, and phylogenetic comparative methods to reconstruct the diet of *N. magdalenensis* by comparing the dental complexity of the first lower molar of *N. magdalenensis* with 25 modern phyllostomid and noctilionid species, covering all major dietary categories. We examined three measures of dental complexity (Bunn et al. 2011; Pineda-Munoz et al. 2017): Dirichlet normal energy (DNE), relief index (RFI), and orientation patch count rotated (OPCR). We also reconstructed the body mass (BM) of *N. magdalenensis* using equations developed for Chiroptera based on body-size measurements (Gunnell et al. 2009). Based on the phylogenetic relationships of *N. magdalenensis* and previous anatomic comparisons, we hypothesize that it was a large-bodied species, less specialized for carnivory than modern carnivorous phyllostomids. We predict sampled carnivores and *N. magdalenensis* to have high DNE and OPCR values and low RFI values, following general trends found in other mammals. Based on previous comparisons of body proportions with modern relatives, we predict *N. magdalenensis*'s BM to be intermediate between those of *C. auritus* (~70 g; Vleut et al. 2019) and *V. spectrum* (~150 g; Amador et al. 2019).

## Methods

The cast of a partial lower left jaw of *Notomycotis magdalenensis* with a complete first molar from the collection of the University of California Museum of Paleontology (UCMP39962) was scanned at the University of New South Wales using a U-CT (Milabs, Utrecht) with 55 kV and 0.17 mA, ultrafocussed setting at a resolution of 30–50  $\mu\text{m}$  (Fig. 1). Our comparative sample consisted of 25 modern noctilionoid bat species of known diet from two noctilionoid bat families (Phyllostomidae and Noctilionidae; Supplementary Table 1). Together, these species represent all major dietary guilds (i.e., carnivory, frugivory, insectivory, nectarivory, omnivory, piscivory, and sanguivory) recognized in bats (Table 1, Fig. 1). For each species, a single lower-left first molar (m1) from adult specimens that did not show excessive wear (no dentine exposed

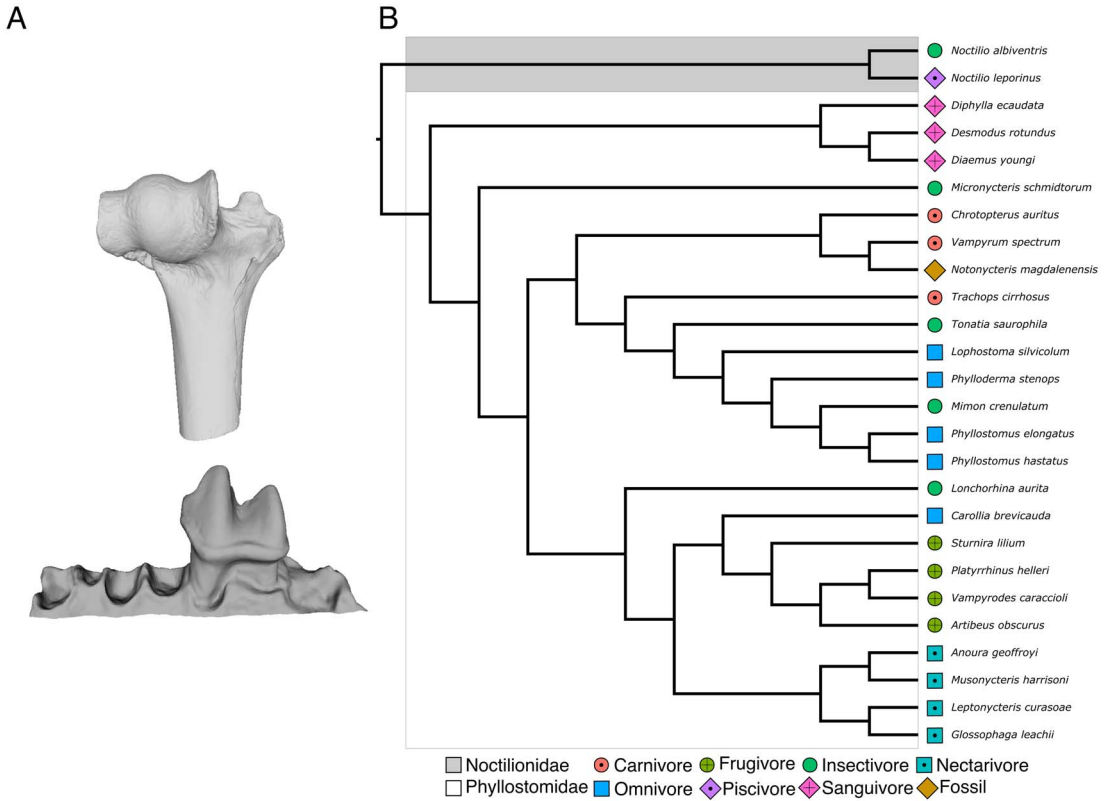


FIGURE 1. Fossil and modern species analyzed in this study. A, Partial humerus (UCMP 38990; left) and lower left jaw (UCMP 39962; right) of *Notonycteris magdalenensis* used in this study for body-mass (BM) reconstruction and dental topography analysis (DTA); B, evolutionary relationships of species analyzed in this study, modified from Dávalos et al. (2014). Tip colors represent dietary guilds and the fossil taxon. (Color online.)

on occlusal view) was analyzed to avoid methodological artifacts in our DTA (Pampush et al. 2016a). Lower molars have been proposed to better reflect food item breakdown, whereas

upper molars better reflect biomechanical stabilization of food items (Berthaume et al. 2020). The 3D models of modern species were retrieved from Shi et al. (2018) based on  $\mu$ CT scans available on MorphoSource, except for an additional 3D model of a lower mandible of *Vampyrum spectrum* provided by S. Santana upon request. Individual m1s were segmented from adjacent teeth and bone using MIMICS v. 20 software (Materialise NV, Leuven, Belgium). Differences in imaging settings and intraspecific variation have been shown to have a negligible effect on DTA analyses (López-Torres et al. 2018; Berthaume et al. 2019b). Additionally, following standard protocols for DTA, individual m1s were cropped below the cingulid to isolate the crown (Pru-frock et al. 2016a; Ungar et al. 2018). Dávalos et al.'s (2014) phylogeny of the Phyllostomidae was pruned to match our sample and used as

TABLE 1. Description of dietary guild classifications used in this study.

Dietary guild	Description
Carnivory	Diet dominated by the consumption of terrestrial vertebrates
Frugivory	Diet dominated by the consumption of fruit
Insectivory	Diet dominated by the consumption of invertebrates
Nectarivory	Diet dominated by the consumption of pollen and nectar
Omnivory	Diet composed of a mix of fruit, pollen, and terrestrial animals
Piscivory	Diet dominated by the consumption of fish
Sanguivory	Diet dominated by the consumption of blood

phylogenetic scaffold for phylogenetic comparative analyses.

**Body-Mass Estimate.**—Based on a dataset of 1160 extant bats, Gunnell et al. (2009) demonstrated that regression analysis of skeletal elements can be an accurate proxy to infer BM in extant and extinct bats, with humeral shaft diameter ( $R^2 = 0.869$ ) and first upper/lower molar area ( $R^2 = 0.818$  and  $0.829$ ) providing best estimates. We used lower first molar area and humeral shaft diameter to reconstruct the BM of *N. magdalenensis* (Gunnell et al. 2009; Hand et al. 2015b, 2016, 2018; Hand and Sigé 2018; Jones et al. 2019). Lower first molar area was calculated from a 3D model of a complete m1 extracted from a fragmented lower left jaw (UCMP 39962). Only fragmented humeral elements have been reported for *N. magdalenensis*, limiting our capacity to obtain measures of mid-shaft diameter. The humeral dorsoventral diameter of the shaft at the distal end of the deltopectoral ridge of a proximal humerus fragment (UCMP 38990) was retrieved from Savage (1951), and the proximal-most shaft diameter of the humerus was extracted from the 3D model of the distal end of a partial humerus (UCMP 38990; Fig. 1). A cast of UCMP 38990 was scanned at the University of New South Wales following the same protocol described earlier. The BM estimate based on m1 size was used to compare *N. magdalenensis* with bats from modern dietary guilds. The BM values for modern bat species were retrieved from the literature (Gunnell et al. 2009; Molinari et al. 2017; Curtis and Santana 2018; Hand et al. 2018; Amador et al. 2019; Jones et al. 2019).

**Dental Topographic Analysis.**—Segmentation and processing practices (e.g., cropping and smoothing) of 3D meshes can impact features of the models (e.g., triangle count and mesh resolution) that are determinant for DTA (Berthaume et al. 2019b). Hence, all meshes were standardized following recommendations for DTA; 3D models were simplified to 10,000 faces and smoothed using 30 iterations with lambda set at 0.6 (Pampush et al. 2016b; Berthaume et al. 2019b). After standardization of meshes, three widely used dental topography metrics were analyzed (Fig. 2): DNE (Bunn et al. 2011), OPCR (Evans et al. 2007), and RFI (Boyer 2008). DNE is a measure of

the degree of curvature of the crown (Fig. 2A); this correlates with shearing capacity and is usually higher in animalivores (Ledogar et al. 2013, 2018; Allen et al. 2015; López-Torres et al. 2018; Ungar et al. 2018). OPCR is an estimate of surface complexity of the crown based on the number of patches facing in the same direction (Evans et al. 2007; Pineda-Munoz et al. 2017; López-Torres et al. 2018; Selig et al. 2020). As for DNE, species with a higher OPCR have more complex tooth surfaces (Fig. 2B), usually associated with more biomechanically demanding diets such as folivory and animalivory (Evans et al. 2007; Cooke 2011; Santana et al. 2011). RFI is a ratio of the 3D and 2D areas of the tooth crown (Fig. 2C) and provides a measure of crown height and, effectively, hypsodonty (Boyer 2008; Cooke 2011; Allen et al. 2015); low RFI values reflect flat crown surfaces commonly found in mammalian frugivores, whereas high values represent tall cusps, such as those found in granivores and insectivores. Incorporating several metrics of dental complexity to inform dietary reconstructions has been suggested to provide more robust characterizations than studies based on a single metric (Pineda-Munoz et al. 2017). All DTAs were performed with the R package molaR (Pampush et al. 2016b).

**Dietary Reconstruction.**—Box plots were used to visually compare values of DNE, OPCR, and RFI in *N. magdalenensis* with those of modern bats of known dietary guilds. A one-way analysis of variance (ANOVA) was used to test for differences in DNE, OPCR, and RFI across our groups. The presence of phylogenetic structuring in our dental complexity data was tested using a multivariate Kmult ( $K-$ ) statistic implemented in the *physignal* function in Geomorph v. 3.2.1 (Adams 2014), using a pruned version of Dávalos et al.'s (2014) phylogeny. Given the strong phylogenetic signal in our dataset, a principal component analysis (PCA, herein morphospace) and a phylogenetic PCA (pPCA, herein phylogeny-corrected morphospace) were performed to reduce the dimensionality of our dental complexity data and visualize patterns of variation, using the *phylo-morphospace* and *phyl.pca* functions of the R package phytools (Revell 2012). A morphospace plot allowed us to elucidate general

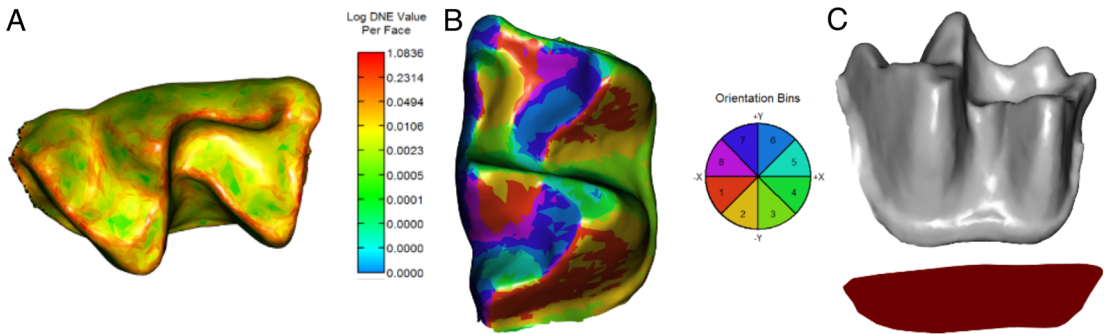


FIGURE 2. Reconstructed meshes showing topographic maps of Dirichlet normal energy (DNE; A), orientation patch count rotated (OPCR; B), and relief index (RFI; C) for the lower m1 of *Notonycteris magdalenensis* (UCMP 39962).

patterns of differentiation across dietary guilds, whereas the phylogeny-corrected morphospace allowed us to discern the influence of phylogenetic kinship in dental complexity variation. A linear discriminant analysis (LDA) was used to classify the diet of *N. magdalenensis* as one of seven dietary guilds, using the *lda* function in the R package MASS. Differences in phylogenetic kinship and patterns of morphological diversity were further explored with a tanglegram to: (1) identify dental complexity similarities between *N. magdalenensis* and other bats of known dietary guilds and (2) detect instances of morphological innovation and convergence across our sample. Loadings of the first two principal components (PC) of the pPCA (explaining >90% of phenotypic variation) were used as phylogeny-corrected phenotypic data. First, the phenotypic dendrogram was built with a hierarchical clustering analysis of the PC loadings, using the *upgma* function in the R package phangorn (Schliep 2011). Next, we compared the position of each species across the phylogeny and morphological dendrogram using the tanglegram produced by the *cophylo* function in the R package phytools (Revell 2012). Parallel lines linking a species across the phylogeny and dendrogram indicate similarities, whereas diagonal links indicate a phylogenetic–phenotypic mismatch.

## Results

**Body-Mass Estimate.**—Depending on the proxy, BM estimates of *Notonycteris magdalenensis* ranged from 53.05 g (m1 area) to 103.39

g (humeral shaft diameter) to 133.35 g (humeral shaft diameter from Savage [1951]). However, a direct measure of humeral diameter at the mid-shaft could not be made (this point is not preserved in fossil material), and this is generally the narrowest point of the bat humerus. Hence, our BM estimates for *N. magdalenensis* based on humeral shaft diameter potentially misestimate BM, so all further analyses and discussion are based on the average of our three estimates (~95 g). Compared with modern species in our sample, the BM of *N. magdalenensis* was greater than the average for frugivores (32.18 g), insectivores (19.23 g), nectarivores (15.2 g), omnivores (46.42 g), and sanguivores (33.36 g), close to the piscivore *Noctilio leporinus* (61 g), and slightly smaller than the average for carnivores (97.74 g; Fig. 3). Compared with its modern relatives, *N. magdalenensis* was larger than *Chrotopterus auritus* (BM = 80 g) and smaller than *Vampyrum spectrum* (BM = 170 g).

**Dietary Differences in Dental Complexity.**—In our sample, nectarivores and sanguivores consistently had the lowest DNE and OPCR values, whereas frugivores and sanguivores had the lowest RFI values (Fig. 4). Omnivores and piscivores had the highest DNE values, followed by frugivores and carnivores (Fig. 4A). Frugivores had the highest OPCR values, followed by carnivores, insectivores, omnivores, and piscivores with very similar values (Fig. 4B). Piscivores and sanguivores had the highest RFI values, followed by carnivores, whereas insectivores and omnivores showed intermediate values (Fig. 4C). Across the three metrics, *N. magdalenensis* overlapped with

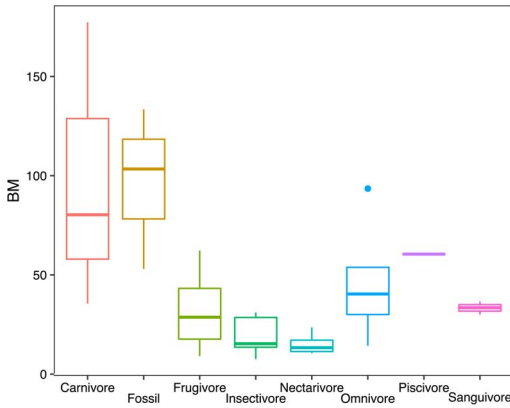


FIGURE 3. Box plots of body-mass (BM) distributions of modern taxa pooled by dietary guilds and BM reconstruction of *Notonycteris magdalenensis* based on m1 area.

values for insectivores and omnivores and showed lower values than its carnivorous close relatives (Fig. 4). One-way ANOVA revealed statistically significant differences in dental complexity metrics across dietary guilds ( $F = 2.46$ ,  $p = 0.05$ ), and the K-statistic revealed a significant phylogenetic signal in our data ( $K = 0.686$ ,  $Z = 2.273$ ,  $p = 0.006$ ).

Dietary groups showed similar patterns of phenotypic variation across morphospace and phylogeny-corrected morphospace (Fig. 5). In morphospace (the first two PCs explained 95.77% of variation), frugivores, nectarivores, and sanguivores occupied non-overlapping regions, whereas carnivores, insectivores, and omnivores overlapped, each showing different

levels of dispersion across morphospace (Fig. 5A). Morphospace also indicates phylogenetic structuring in morphological variation and dietary specializations, with desmodontines (all sanguivores), glossophagines (all nectarivores), and stenodermatines (all frugivores) occupying exclusive areas in morphospace. Species showed a similar arrangement in phylogeny-corrected morphospace (Fig. 5B). Frugivores, nectarivores, and sanguivores occupied unique subspaces, and carnivores, insectivores, and omnivores overlapped around the origin. The specialized piscivore *N. leporinus* always separated from all other guilds, but the omnivore *Noctilio albiventris* overlapped in morphospace with other animalivore guilds. Across morphospaces, *N. magdalenensis* was always nested within the insectivore subspace, close to the omnivore subspace and outside the carnivore subspace.

**Dietary Reconstruction.**—The tanglegram showed a similar placement of the piscivore, two carnivores, and one insectivorous species in the phylogeny and dendrogram and a consistent clustering of sanguivorous and nectarivorous taxa (Fig. 6). A mismatch between the placement of *N. magdalenensis* in the phylogeny and phenotypic dendrogram was also evident. The phenotypic dendrogram clustered *N. magdalenensis* with the insectivorous *Lonchorhina aurita*, and these two were clustered with the omnivorous *Phylloderma stenops* in our sample.

LDA correctly classified 68% of modern species in our sample into their dietary guilds when all three DTA metrics were analyzed,

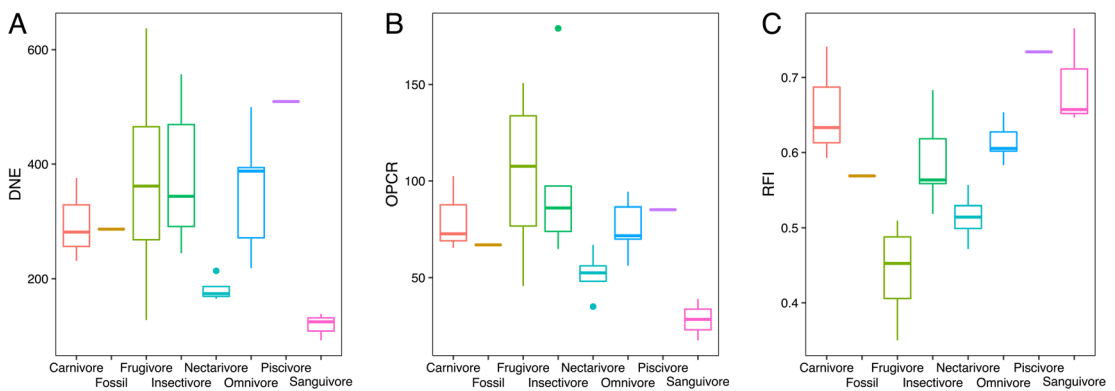


FIGURE 4. Box plots of dental topography analysis (DTA) results for Dirichlet normal energy (DNE; A), orientation patch count rotated (OPCR; B), and relief index (RFI; C) of modern taxa pooled by dietary guilds and *Notonycteris magdalenensis*.

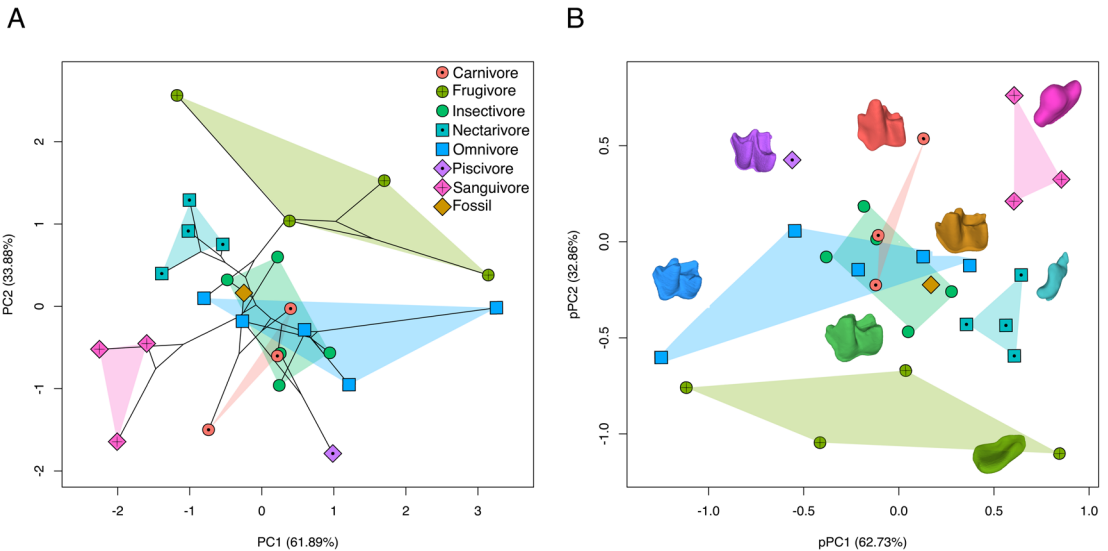


FIGURE 5. Morphospace (PCA; A) and phylogeny-corrected morphospace (pPCA; B) based on dental topography analysis (DTA: Dirichlet normal energy [DNE], orientation patch count rotated [OPCR], and relief index [RFI]). Dot colors represent dietary guild categories (carnivory, frugivory, insectivory, nectarivory, omnivory, piscivory, sanguivory) and fossil species (*Notonycteris magdalenensis*). The 3D models of m1 illustrate dental diversity in sampled taxa, colors matching dietary and fossil categories: carnivory (*Phyllostomus hastatus*), frugivory (*Sturnira bogotensis*), insectivory (*Miconycteris schmidtorum*), nectarivory (*Musonycteris harrisoni*), omnivory (*Lophostoma silvicolium*), piscivory (*Noctilio leporinus*), sanguivory (*Desmodus rotundus*), and fossil (*N. magdalenensis*). (Color online.)

and 40% of modern species when only DNE and OPCR were analyzed (Table 2). When DNE, OPCR, and RFI were combined, 100% of frugivores, nectarivores, piscivores, and sanguivores were correctly classified, followed by omnivores (80%) and insectivores (20%). Excluding RFI from the LDA decreased the accurate classification of frugivores by 75%, of omnivores by 40%, of nectarivores by 25%, and of insectivores by 20%. Both iterations of LDA classified *N. magdalenensis* as an omnivore–insectivore, with a posterior probability of 34.46% and 27.57% (using all metrics) and 21.92% and 14.75% (excluding RFI). LDA excluding RFI recovered a 21.99% posterior probability of *N. magdalenensis* being a carnivore. Both iterations of LDA failed to correctly classify all modern carnivores, with 33.33% classified as omnivores, 33.33% as insectivores, and 33.33% as sanguivores. Nevertheless, carnivory had the second-highest posterior probability (>15%) across all modern carnivores (Supplementary Table 2). In contrast, carnivory had the fourth-highest LDA posterior probability (10.04%) when classifying *N. magdalenensis*'s diet.

## Discussion

DTA reconstructed the diet of *Notonycteris magdalenensis* as an omnivorous or insectivorous species and distinct from its modern sister taxa *Chrotopterus auritus* and *Vampyrum spectrum*, both of which are carnivores. BM estimates suggest that *N. magdalenensis* was a large-bodied bat (~95 g), larger than most modern phyllostomids and bats in general (Gunnell et al. 2009), but smaller than its largest modern relative *V. spectrum*. The reconstructed diet and BM of *N. magdalenensis* suggest this species could represent a transitional stage between small-bodied ancestral insectivorous phyllostomids (Simmons et al. 2020) and large, specialized modern carnivores, illustrating the importance of body-size increases for the evolution of carnivory in Chiroptera (Santana and Cheung 2016; Giannini et al. 2020). DTA offers an additional tool to help reconstruct and differentiate dietary niches in bats.

*Dental Topography Analysis and Dietary Specializations in Bats.*—Functional demands associated with the biomechanical processing of food have been linked to morphological adaptations of the feeding apparatus and sensory



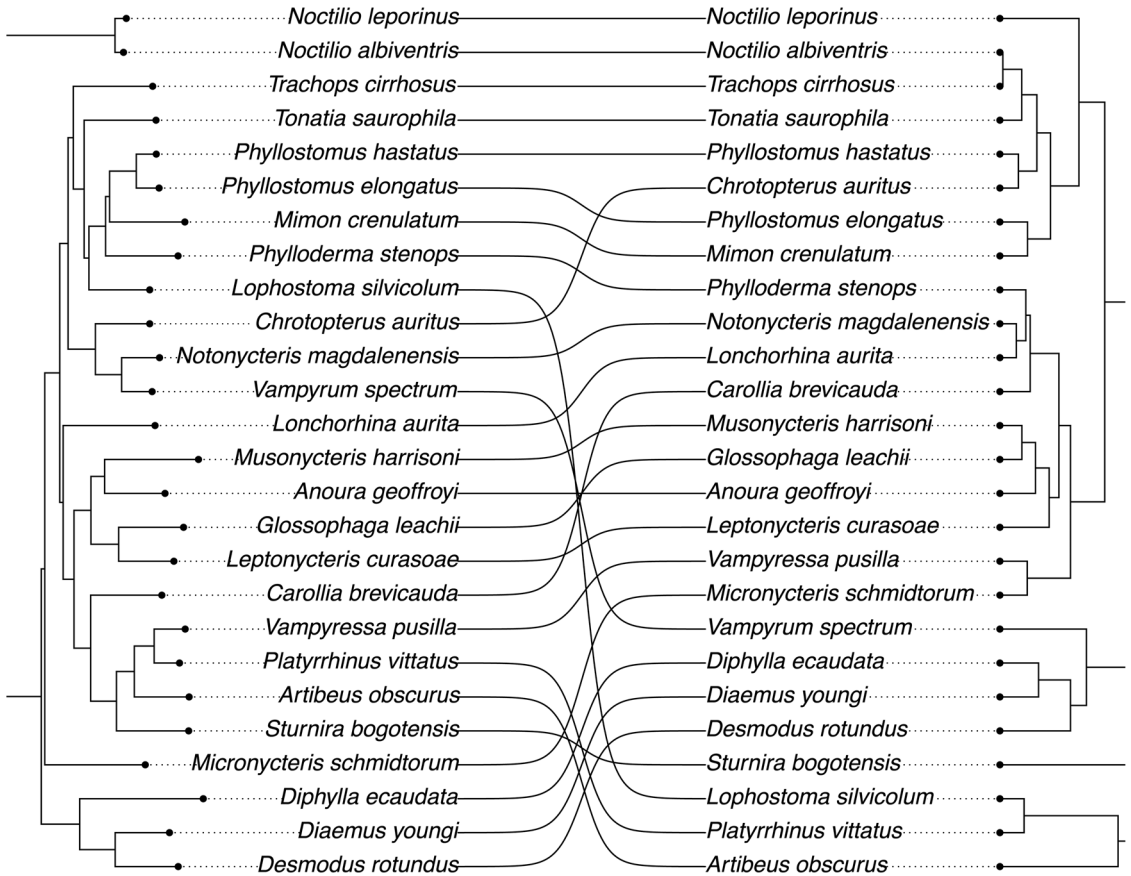


FIGURE 6. Tanglegram of evolutionary relatedness (left) and phenotypic dendrogram (right) of bat dental complexity. Lines indicate the change in position of the same species in both panels.

organs in bats (Nogueira et al. 2009; Santana et al. 2010, 2012; Jacobs et al. 2014; Arbour et al. 2019; Rossoni et al. 2019; Brokaw and Smotherman 2020; Leiser-Miller and Santana 2020). Food item hardness has been linked with the robustness of the jaw and the length of the rostrum (Freeman 1981, 1998, 2000; Arbour et al. 2019). Studies have also found evidence suggesting dietary adaptations correlate with postcranial morphological differences, revealing the interaction between diet (i.e., food processing) and locomotion (i.e., foraging strategies) has an overarching effect on the ecomorphology of bats (Norberg and Rayner 1987; Morales et al. 2019; Gaudioso et al. 2020; López-Aguirre et al. 2021). Scapular morphology in bats has been correlated with the convergent evolution of dietary adaptations (Gaudioso et al. 2020). Dental morphology has been

shown to have both a phylogenetic signal and an ecological signal, reflecting evolutionary relatedness as well as ecological differences within Chiroptera (e.g., Hand 1985, 1996, 1998; Freeman 1988, 1995, 2000; Santana et al. 2011; Self 2015; Simmons et al. 2016; Zuercher et al. 2020). Our results also detected a dual phylogenetic and ecological signal in dental complexity variation, which highlights DTA as a potential tool in the study of dental ecology and evolution in bats. Santana et al. (2011) used orientation patch count to assess diet-based ecomorphological differences between noctilionoid bats. By applying DNE, OPCR, and RFI, ours is the first study to apply multivariate DTA to investigate bats, fossil and living. There is potential for future studies to explore a variety of ecological and evolutionary questions, including the many cases of convergent

TABLE 2. Predicted dietary guild classification based on linear discriminant analyses (LDAs) analyzing Dirichlet normal energy (DNE), orientation patch count rotated (OPCR), and relief index (RFI) (ALL) and excluding RFI (DNE+OPCR).

Species	Dietary category	Predicted ALL	Predicted DNE+OPCR
<i>Anoura geoffroyi</i>	Nectarivore	Nectarivore	Nectarivore
<i>Artibeus obscurus</i>	Frugivore	Frugivore	Frugivore
<i>Carollia brevicauda</i>	Omnivore	Omnivore	Nectarivore
<i>Chrotopterus auritus</i>	Carnivore	Insectivore	Frugivore
<i>Desmodus rotundus</i>	Sanguivore	Sanguivore	Sanguivore
<i>Diaemus youngi</i>	Sanguivore	Sanguivore	Sanguivore
<i>Diphylla ecaudata</i>	Sanguivore	Sanguivore	Sanguivore
<i>Glossophaga leachii</i>	Nectarivore	Nectarivore	Nectarivore
<i>Leptonycteris curasoae</i>	Nectarivore	Nectarivore	Sanguivore
<i>Lonchorhina aurita</i>	Insectivore	Nectarivore	Carnivore
<i>Lophostoma silvicolium</i>	Insectivore	Insectivore	Frugivore
<i>Micronycteris schmidtorum</i>	Insectivore	Nectarivore	Omnivore
<i>Mimon crenulatum</i>	Insectivore	Omnivore	Piscivore
<i>Musonycteris harrisoni</i>	Nectarivore	Nectarivore	Nectarivore
<i>Noctilio albiventris</i>	Omnivore	Omnivore	Omnivore
<i>Noctilio leporinus</i>	Piscivore	Piscivore	Piscivore
<i>Phyllostoma stenops</i>	Omnivore	Carnivore	Carnivore
<i>Phyllostomus elongatus</i>	Omnivore	Omnivore	Piscivore
<i>Phyllostomus hastatus</i>	Omnivore	Omnivore	Omnivore
<i>Platyrrhinus vittatus</i>	Frugivore	Frugivore	Insectivore
<i>Sturnira bogotensis</i>	Frugivore	Frugivore	Nectarivore
<i>Tonatia saurophila</i>	Insectivore	Carnivore	Frugivore
<i>Trachops cirrhosus</i>	Carnivore	Omnivore	Omnivore
<i>Vampyressa pusilla</i>	Frugivore	Frugivore	Carnivore
<i>Vampyrum spectrum</i>	Carnivore	Sanguivore	Nectarivore
<i>Notonycteris magdalenensis</i>		Omnivore	Carnivore

diets between different bat clades (e.g., frugivory, nectarivory, and carnivory) and the reconstruction of ancestral states to investigate dietary diversification in Chiroptera. Our results of DTA-based LDA for carnivorous bats contrast with previous studies analyzing carnivorous crocodylomorphs (Melstrom and Irmis 2019) and non-volant mammals (Pineda-Munoz et al. 2017) that revealed a greater differentiation of this diet. One possible explanation is that our approach was based on a single tooth, due to the nature of the *N. magdalenensis* fossil material, whereas previous studies analyzed whole tooththrows, possibly capturing a greater suite of dental specializations. Also, it is possible that the presence of other non-dental adaptations for carnivory in bats (e.g., cranial specializations and foraging strategies) are significant, relaxing the selective pressures on dental complexity (Norberg and Fenton 1988; Santana and Cheung 2016).

Our study focused on reconstructing the likely diet of the extinct phyllostomid *N. magdalenensis* by comparing its dental morphology with that of modern members of this family. Phyllostomidae is recognized as the greatest

adaptive radiation of any mammalian family (Monteiro and Nogueira 2011; Rossoni et al. 2017; Fleming et al. 2020). Adoption of novel dietary niches and morphological innovation have been linked to the diversification of this family (Freeman 2000; Dumont et al. 2012; Rossoni et al. 2019; Hedrick et al. 2020). Representing less than 15% of modern global bat diversity (~200 species), phyllostomid bats have successfully colonized almost every dietary niche found in the entire chiropteran order, with the exception of piscivory (Monteiro and Nogueira 2011; Rossoni et al. 2017; Fleming et al. 2020). Previous studies have suggested that different phyllostomid clades adapted to nectarivory convergently, reflecting the ecomorphological evolvability in phyllostomids (Datzmann et al. 2010; Rojas et al. 2016). Low DNE and OPCR values found in our sanguivorous and nectarivorous bats indicate evolutionary convergence of reduced occlusal curvature in species with liquid diets. Loss or reduction of incisors and cheek teeth have been identified as convergent adaptations to liquid diets in Chiroptera (e.g., Freeman 1988, 1998; Bolzan et al. 2015; Berkovitz and Shellis

2018). Nevertheless, sanguivorous and nectarivorous bats also show divergent specialized cranial morphologies adapted to each diet, with these dietary innovations following different evolutionary trajectories (Rossoni et al. 2017, 2019). Sanguivorous bats have a short rostrum, enlarged and procumbent upper incisors adapted for slicing, and reduced cheek teeth and lower incisors (Berkovitz and Shellis 2018). Nectarivorous bats exhibit elongated rostra and reduction or loss of incisors and modified cheek teeth (Freeman 1988, 1995). This divergence is also reflected in marked differences in RFI values between sanguivores and nectarivores and non-overlapping regions occupied in morphospace (Fig. 5). High RFI values found in sanguivorous bats reflect the reduction of molar width during the evolution of liquid diets in bats.

A previous study of dental complexity in bats found higher orientation patch count (an index of topographic complexity prior to OPCR) in frugivores compared with insectivores and omnivores (Santana et al. 2011), unlike the pattern recorded in rodents and primates (Evans et al. 2007; Winchester et al. 2014; López-Torres et al. 2018; Selig et al. 2019, 2020). Our results (i.e., high OPCR in frugivores compared with animalivores and omnivores) capture the uniquely complex teeth of frugivorous phyllostomid bats compared with other frugivorous mammals, including pteropodid bats. Non-phyllostomid frugivorous mammals tend to have flatter occlusal surfaces due to reduced shearing surfaces (e.g., cusps and crests), whereas the lower molars of phyllostomid frugivores retain a labial crest formed by the metaconid and paraconid (Berkovitz and Shellis 2018). Frugivorous species in our sample had the lowest RFI values of any dietary group, showing low-crowned teeth similar to those in other mammalian groups (Boyer 2008; Bunn and Ungar 2009; Prufrock et al. 2016b). Carnivorous and piscivorous species occupied different sub-regions of morphospace, indicating demands of feeding on terrestrial and aquatic vertebrates shaped dental complexity differentially in each group. Cranial morphology of piscivorous bats has been found to be significantly different from other animalivorous bats, possibly due to differences in the masticatory and foraging biomechanics between both groups (Santana and

Cheung 2016). Future studies could expand to include a wider range of bat species and families to test convergent evolution between more distantly related taxa.

*Dietary and Body-Mass Reconstruction of *Notonycteris magdalenensis*.*—Our inferences of the diet and BM of *N. magdalenensis* may have bearing on broader understanding of the evolution of carnivory in Phyllostomidae. Some studies have estimated that carnivory had evolved in Phyllostomidae by at least the middle Miocene, based on the dental morphology of *N. magdalenensis* (Savage 1951; Czaplewski et al. 2003; Simmons et al. 2020). Further comparisons of measurements of cranial and postcranial remains have been used to suggest this species was larger than *C. auritus* but smaller than *V. spectrum* (Savage 1951; Czaplewski et al. 2003; Simmons et al. 2020). Giannini et al. (2020) explored the evolution of BM in extant noctilionoid bats, including all of the phyletic lineages and dietary modes exhibited by them. These authors hypothesized that body-size stability early in the evolution of phyllostomids provided great potential for size increases and decreases. They suggest that the increase in BM that enabled specialized carnivory, ultimately resulting in the very large bodied Vampyrini (*C. auritus* and *V. spectrum*), probably occurred relatively late (late Miocene rather than the middle Miocene; molecular divergence dating of Amador et al. [2016]), which is after the time of the La Venta fauna and of *N. magdalenensis*. Our results suggest that *N. magdalenensis* may have been a large insectivore or omnivore, with an intermediate BM between insectivores and carnivores in our sample, and are concordant with (or at least, do not refute) a later appearance of specialized carnivorous phyllostomids.

In our DTA study, *N. magdalenensis* had lower values of DNE, OPCR, and RFI than the modern carnivores and piscivores in our sample, indicating lower occlusal curvature, dental complexity, and crown height (i.e., lesser capacity to slice vertebrate prey). LDA classified *N. magdalenensis* primarily as an omnivore (posterior probability of 34.46%), and secondarily as an omnivore (posterior probability of 27.57%), whereas there was only a 10.04% posterior probability of

carnivory. Our tanglegram based on the same data also suggests an omnivorous or insectivorous diet for *N. magdalenensis*, which groups within a cluster of omnivorous and insectivorous species, distant from carnivores or its sister taxa. Based on our results, we hypothesize that *N. magdalenensis* represents a transitional form between modern carnivory and the ancestral insectivore state.

Moreover, an omnivorous or insectivorous diet for *N. magdalenensis* also supports the observations by Savage (1951) and Czaplewski et al. (2003). Their qualitative studies of the dentition of *N. magdalenensis* found that dental features in *N. magdalenensis* typically observed in carnivorous bats (Freeman 1988, 1998) were not as highly developed as those same features in its living relatives *V. spectrum* and *C. auritus*, suggesting that *N. magdalenensis* probably had a less carnivorous diet than its modern relatives. These features include relatively lower crown height in *N. magdalenensis*, more robust crests and cusps, less reduced talonids in lower molars, less obliquely oriented ectoloph crests, and shorter postmetacristae in upper molars (Czaplewski et al. 2003).

With the exception of *Trachops cirrhosus* (~35 g), all carnivorous phyllostomids have average BMs higher than 80 g, well above the average for any other diet (Norberg and Fenton 1988; Santana and Cheung 2016; Moyers Arévalo et al. 2020). *Vampyrum spectrum*, thought to be the closest living relative of *N. magdalenensis*, is the largest bat in the New World (BM ~170 g) and is regarded as an example of the coevolution of increased body size and carnivory in Phyllostomidae (Arévalo 2020; Moyers Arévalo et al. 2020). Our estimate of BM for *N. magdalenensis* (~95 g) based on m1 area indicates that this species was larger than most insectivores and within the range of carnivorous phyllostomids. In agreement with our DTA, this could indicate that *N. magdalenensis* was not a specialized carnivore and could have instead had an insectivorous or omnivorous diet, similar to other omnivorous, large-bodied Miocene noctilionoid species (Hand et al. 2015a, 2018). Other studies have estimated phyllostomid BM ancestral state range as between 11–12 g, close to the ancestral state for Noctilionoidea (9–12 g) and modern

Chiroptera (12–14 g) (Giannini et al. 2012, 2020; Arévalo 2020; Moyers Arévalo et al. 2020). This suggests relative evolutionary stasis in body size during the early evolution of modern bat families, most of which had evolved and/or had appeared in the fossil record before the early Oligocene (~35 Ma) (Giannini et al. 2012; Arévalo 2020; Moyers Arévalo et al. 2020). Within Phyllostominae, a significant shift to an increased size of more than 50 g has been recovered for the clade including *C. auritus* and *V. spectrum* (divergence dated at around 16 Ma), highlighting a rapid gain of >30 g in the first 10 Myr following the origin of Phyllostomidae (Arévalo 2020). Based on the age of the La Venta bat fauna (13–12 Ma), *N. magdalenensis* can be interpreted as fossil evidence for this evolutionary increase in body size within Phyllostominae (Arévalo 2020), and we propose it represents a transitional stage of body size between the small insectivorous phyllostomid ancestor and the large modern carnivorous phyllostomids (Datzmann et al. 2010; Baker et al. 2012). Taking our DTA and BM reconstruction together, we hypothesize that during the evolution of carnivory in Phyllostomidae, increased body size predated dental specializations.

Carnivory in phyllostomids is thought to have evolved convergently at least twice from an insectivorous common ancestor (Wetterer et al. 2000; Hoffmann et al. 2008; Baker et al. 2012, 2016). The convergent evolution of carnivory in Chiroptera has been studied at the ordinal level (evolving at least six times; e.g., Norberg and Fenton 1988; Datzmann et al. 2010; Santana and Cheung 2016) and the family level (evolving at least twice in Megadermatidae; e.g., Hand 1985, 1996). Independent evolutionary shifts to increasing body size in Vampyrini and Phyllostomini from a smaller phyllostomid ancestor also support two instances of convergent evolution of carnivory (Arévalo 2020). Similarities in DTA between carnivorous species of both tribes in our study indicate they converged in the same morphospace.

*La Venta Bat Community*.—Authors of paleoecological reconstructions have inferred the La Venta paleoenvironment to have been a warm, wet, and aseasonal mosaic woodland, possibly with patches of open grasslands and riverine systems (Kay and Madden 1997; Croft 2001;

Spradley et al. 2019). Paleogeographic models of the eastern Andean cordillera suggest La Venta had a paleoelevation of <200 m, reflecting a lowland trans-Andean ecosystem that acted as a portal between the Andes and Central Andes (Hoorn 1994; Hoorn et al. 1995; Guerrero 1997; Montes et al. 2021). Precipitation has been estimated in the range of 1500–2000 mm and temperatures around 20°C–25°C, similar to the conditions found in modern forests of the Andes–Amazonian transition of tropical South America (Kay and Madden 1997; Spradley et al. 2019). This type of transitional ecosystem is characterized by rich taxonomic diversity and high endemism, possibly due to reciprocal faunal exchange between highland and lowland tropical faunas since the Miocene (Upham et al. 2013).

The fossil bat community is also informative for paleohabitat reconstructions of La Venta and supports the presence of mosaic woodlands. Two modern species of foliage-roosting species (*Thyroptera* spp.) typical of lowland tropical forests have been reported from La Venta, indicating the presence of *Heliconia*-like vegetation (Czaplewski et al. 2003). The presence of the trawling insectivore *N. albiventris* in the La Venta fossil fauna/community also indicates the presence of bodies of water in the ecosystem (Kalko et al. 1998). Although this species is mainly an insectivore, some of its features (enlarged feet and constant frequency echolocation) have been interpreted as pre-adaptations for piscivory (Kalko et al. 1998), supported by different studies reporting the consumption of insects, fruit, and pollen by *N. albiventris* (Fernando et al. 2007). Dietary reconstruction of La Venta's *Palynephyllum antimaster* indicates it was an omnivore that included nectar in its diet (Yohe et al. 2015). Our dietary reconstruction for *N. magdalenensis* and a previous reconstruction for *P. antimaster* (Yohe et al. 2015) corroborate the hypothesized mosaic woodland ecosystem of La Venta, with a mixture of high-canopy trees and understory flowering vegetation (Kay and Madden 1997).

The 14 bat species recorded from La Venta would have occupied at least three dietary niches (insectivory, omnivory, and nectarivory), occupying the trawling, gleaning, and hawking aerial guilds. They occupied a wide body-size range (4–90 g), implying an

ecologically diverse community (Czaplewski et al. 2003). Our results indicate *N. magdalenensis* was the largest known noctilionoid bat in the La Venta fauna, although BM reconstructions of the other extinct species would better elucidate the trophic structure of the bat community. The interpretation of *Noctilio leporinus*, *P. antimaster*, and *N. magdalenensis* as transitional forms (Paván et al. 2013; Yohe et al. 2015; Simmons et al. 2020) suggests ecosystems like La Venta may have been important for the evolution of dietary innovations (i.e., carnivory, insectivory, and nectarivory) in Phyllostomidae (Kalko et al. 1998; Yohe et al. 2015). Additional study of the La Venta bat fauna is expected to further inform hypotheses regarding the evolution of Phyllostomidae, the most ecologically diverse family of mammals.

## Conclusions

We used DTA and a quantitative comparative approach to reconstruct the diet of the phyllostomine *Notonycteris magdalenensis* from the middle Miocene La Venta fauna (tropical South America), the most diverse fossil bat community in South America. Our study investigated patterns of dental complexity (DNE, OPCR, and RFI) variation across seven dietary guilds and provided the first multivariate DTA in Chiroptera. We found strong differentiation in dental complexity between dietary guilds, indicating that DTA is an informative tool to study ecomorphology in bats. Applying phylogenetic comparative methods, we found statistical support for the presence of both ecological and phylogenetic signal in the variation of molar complexity. Our results suggest *N. magdalenensis* was an omnivore or insectivore, rather than a carnivore like its extant sister taxa *Chrotopterus auritus* and *Vampyrum spectrum*. Based on our BM reconstructions of *N. magdalenensis* (~95 g), we infer it was the largest predatory bat in La Venta, being larger than most modern insectivorous bats and within range of modern carnivorous bats. Combining our diet and BM reconstructions, we interpret *N. magdalenensis*'s BM and dental topography to represent pre-adaptations associated with the colonization of a carnivorous niche. Our results confirm that *N. magdalenensis* was

probably not a specialized carnivore. Evidence that modern carnivory (typically associated with a large BM and specialized cranial morphology) had evolved in Phyllostomidae by the middle Miocene remains to be demonstrated.

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### Data Availability Statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.pnvx0k6mt>.

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