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Dental Variation in Megabats (Chiroptera: Pteropodidae): Tooth Metrics Correlate with Body Size and Tooth Proportions Reflect Phylogeny

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Abstract

Variation in the dentition yields insight into the evolutionary history of Mammalia. However, to date, there has been limited research on the dental variation in Pteropodidae, a family of bats found throughout sub-Saharan Africa, Southeast Asia, and Oceania. Most species are large, diurnal, non-echolocating, and eat fruit or nectar. Pteropodids are of significant concern in conservation due to rapidly declining populations resulting from habitat loss, climate change, and their impacts on agriculture and disease. We collected dental metrics from the mandibular postcanine teeth of 101 pteropodid specimens spanning six species within the family to test three hypotheses: H1) dental metrics are significantly different across pteropodid species; H2) variation in pteropodid dental metrics is associated with variation in body size; and H3) variation in pteropodid dental proportions is associated with phylogenetic relatedness. We find that dental linear metrics vary significantly across pteropodids and are significantly associated with body size. In contrast, dental proportions of pteropodids reflect phylogenetic relationships. We propose that the combination of approaches for quantifying postcanine dental variation can elucidate and refine our understanding of the various selective forces that shaped the Pteropodidae radiation.

Introduction

Bats (Chiroptera) are the only true flying mammals, allowing them to travel quickly and find food aerially (Norberg and Rayner 1987; Thewissen and Babcock 1992; Teeling et al. 2000). Most echolocate to detect food and identify their surroundings at night (Neuweiler 1984; Teeling et al. 2000;

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Willig et al. 2003; Simmons 2005b). Molecular analyses estimate the most recent common ancestor of extant bats to be approximately 62 million years old, and the oldest fossil of a bat capable of flight is dated to around 53 million years ago (Cao et al. 2000; Speakman 2001; Teeling et al. 2005; Arnason et al. 2008; Simmons et al. 2008; Agnarsson et al. 2011). Since the evolution of flight, this monophyletic order has undergone a massive radiation with species now present on every continent except Antarctica (Jepsen 1970; Koopman and Cockrum 1984; Baker et al. 1991; Thewissen and Babcock 1992; Simmons 2005a; Teeling et al. 2005; Agnarsson et al. 2011). Bats occupy a wide variety of habitats (Jepsen 1970; Simmons 2005b; Eklöf and Rydell 2017), often in abundance, with some species roosting in colonies of over one million (e.g., *Tadarida brasiliensis* in the southwestern United States; Keeley and Keeley 2004; Betke et al. 2008). In tandem with this geographic and ecological radiation, bats evolved diverse dietary strategies with different species specializing on insects, blood, fruit, nectar, and small vertebrates (Wilson 1973; Smith 1976; Freeman 1979; Thewissen and Babcock 1992; Nowak et al. 1994; Freeman 1995, 1998; Phillips 2000).

Chiroptera is the second most speciose extant mammalian order, consisting of nearly a quarter of all extant mammalian species (Simmons 2005b; Giannini et al. 2006). Molecular analyses have organized the chiropteran phylogeny (Fig. 1) into suborders Yinpterochiroptera and Yangochiroptera; megabats are grouped as a monophyletic clade within Yinpterochiroptera, as sister clade to five families of microbats (Teeling et al. 2000, 2005; Springer et al. 2001; Simmons 2005a; Jones and Teeling 2006; Arnason et al. 2008; but see: Agnarsson et al. 2011). The term megabat is commonly used interchangeably with Old World fruit bats, flying foxes, and the taxonomic designation Pteropodidae (Simmons 2005a; Agnarsson et al. 2011; Almeida et al. 2011).

Pteropodidae is one of the most speciose families within Chiroptera. It has an exclusively African, Eurasian, and Oceanic distribution and is distinct from other families within Chiroptera by a lack of laryngeal echolocation and the evolution of large body size (Mickleburgh et al. 1992; Kirsch et al. 1995; Teeling et al. 2000, 2005; Agnarsson et al. 2011; Almeida et al. 2011; Hulva et al. 2012). Paleontological and molecular data indicate that the pteropodid lineage split from other bats approximately 58 million years ago (Jones et al. 2005; Teeling et al. 2005; Arnason et al. 2008; Teeling 2009; Agnarsson et al. 2011; Almeida et al. 2011; Shi and Rabosky 2015; Amador et al. 2018), and the pteropodid crown group has increased significantly in body size over the last 26 million years (Kirsch et al. 1995; Jones et al. 2005; Teeling et al. 2005; Teeling 2009; Agnarsson et al.

2011; Almeida et al. 2011, 2014; Shi and Rabosky 2015; Amador et al. 2018; Arévalo et al. 2020). The most dramatic chiropteran body mass increases have been identified at megabat nodes, and particularly at the *Pteropus* node where the species are estimated to now be 417% the size of the common ancestor of extant bats (Teeling et al. 2005; Simmons et al. 2008; Giannini et al. 2012).

Pteropodids are the largest bats and can weigh over one kilogram with a wingspan of up to one and a half meters (Nowak et al. 1994). Their generally large body size may impact migration, foraging, torpor, and other energetically costly activities (McNab and Bonaccorso 2001; Giannini et al. 2012). Males are usually larger than females, with body mass differences hypothesized to be due to either intrasexual competition or minimizing energetic costs for females during reproduction, as females are solely responsible for rearing young (Walker et al. 2004; Storz et al. 2001; Giannini et al. 2006; Rahman and Abdullah 2010; Benda et al. 2012). Body size in these bats is positively correlated with fruit size suggesting strong selection on the relationship between body size and diet (Fleming et al. 1987; Campbell et al. 2007). It has been hypothesized that increasing body size, dietary change, and less frequent roosting in caves are associated with the loss of laryngeal echolocation in megabats (Teeling et al. 2000; Giannini et al. 2012). Although no pteropodids echolocate laryngeally, some do produce sonar clicks via lingual echolocation or wing clapping perhaps as an adaptation for easier navigation in caves where they roost colonially (Gould 1988; Funakoshi et al. 1995; Speakman 2001; Yovel et al. 2011; Schoeman and Goodman 2012; Nesi et al. 2013; Boonman et al. 2014). While primarily frugivorous, some megabats are specialists on certain fruits or nectar, while others are generalists, even occasionally consuming insects (Birt et al. 1997; Kirsch and Lapointe 1997; Banack 1998; Dumont 2003; Barclay et al. 2006). Frugivory and nectarivory are not mutually exclusive and are often seasonal (Birt et al. 1997; Dumont 1997; Kirsch and Lapointe 1997; Eby 1998; Freeman 1998). Some pteropodid species prefer fruit but facultatively eat nectar, leaves, or blossoms, and vice versa (Kirsch and Lapointe 1997; Tan et al. 1998). There is a lot of variation in dietary preferences even within a species, as some individuals may prefer fruits while others prefer other vegetation (Birt et al. 1997).

Like most other mammals, bats have diphyodont dentition, with permanent teeth replacing the deciduous dentition during ontogeny (Popa et al. 2016). Variation in the size and shape of bat dentitions correlates broadly with major dietary strategies. Insectivorous bats have classically dilambdodont dentition with precise occlusion for crushing insect chitin and sharp shearing edges (Smith 1976; Freeman 1979, 1998; Santana et al. 2011). Primarily frugivorous microbats (family Phyllostomidae, occurring only in the Americas) and megabats have fewer, smaller, blunter teeth with complex

Fig. 1 Phylogeny of extant bats. Pteropodidae is represented by three genera and six species. All other families are represented by a single species except Vespertilionidae (represented by both *Myotis lucifugus* and *Lasiurus cinereus*), and Cistugidae, Nycteridae, and Rhinonycteridae (for which molecular data were not available). No molecular data were available for *Pteropus yapensis*. However, some researchers consider *P. yapensis* to be a subspecies of *P. mariannus* (Mickleburgh et al. 1992; Wiles 2005; Brown et al. 2011), with an estimated divergence time of 0.38 million years (Almeida et al. 2014), and so we used molecular data for *P. mariannus* instead

molars for crushing plant material and a fused mandibular symphysis (Thewissen and Babcock 1992; Freeman 1998; Santana et al. 2011). In contrast, primarily nectarivorous bats tend to have rough tongues, reduced dentition, and longer, thinner rostrums (Freeman 1988, 1995, 1998; Kitchener et al. 1990; Birt et al. 1997; Dumont 1997; Kirsch and Lapointe 1997; Phillips 2000). Carnivorous bat species that eat fish, bats, and other small vertebrates have evolved distinctively larger upper molars and specialized braincases (Freeman 1998). Hematophagous bats have perhaps the most unique craniodental morphology with wide palates, specialized incisors, and reduction of postcanine dentition (Greenhall 1972; Freeman 1998; Santana et al. 2012).

Within Pteropodidae, craniodental morphology has been shown to play an essential role in ecological and dietary adaptations (Freeman 1995, 1998; Phillips 2000; Aguirre et al. 2003; Dumont 2004). But that said, outside of studies of sexual dimorphism (see: Nowak et al. 1994; Storz et al. 2001; Giannini et al. 2006; Rahman and Abdullah 2010; Benda et al. 2012) and notes on dental anomalies (see: Bergmans 1976; Juste and Ibáñez 1993; Giannini and Simmons 2007; Lanza et al. 2008), very little is known about variation in pteropodid dental morphology. Given that the study of mammalian dental morphology and proportions continues to provide insight into taxonomy, diet, behavior, life history, and evolution of the order (e.g., Lucas 2004; Wilson 2013; Hlusko et al. 2016; Monson et al. 2019), an investigation of dental variation within Pteropodidae promises to add to our understanding of this family. To address this gap in the Pteropodidae literature, we measured the dentition of 101 megabats, spanning six species, to test three hypotheses:

H1) Pteropodid dental metrics and proportions distinguish taxa;

H2) Variation in pteropodid dental metrics is associated with variation in body size (as captured by body mass and forearm length); and,

H3) Variation in pteropodid dental proportions is associated with phylogenetic relatedness.

Materials and Methods

Materials

We measured the dentition of 101 skeletonized individuals within Pteropodidae (Table 1). These specimens span three genera and six species: *Dobsonia minor* Dobson, 1879, *Dobsonia moluccensis* Quoy and Gaimard, 1830, *Pteropus conspicillatus* Gould, 1850, *Pteropus woodfordi* Thomas, 1888, *Pteropus yapensis* Andersen, 1908, and *Rousettus amplexicaudatus* Geoffroy, 1810 (See Fig. 2 for three representative taxa). All specimens are held in the Museum of Vertebrate Zoology at the University of California,

Berkeley, and were collected from tropical regions of Southeast Asia and Oceania with the majority collected from Papua New Guinea (PNG).

To investigate the relationship between body size and dental variation in pteropodids, we collected data on body mass and forearm length from the published literature for all species of Pteropodidae represented in our sample ($n = 6$), as well as for the other, non-pteropodid species represented in our extant phylogeny of bats ($n = 17$; Supporting Information Appendix A). The authors of PanTHERIA (our reference dataset) collected these data from a thorough literature review (Jones et al. 2009). It is important to note that data collected from the literature are susceptible to interobserver error, and future work focused on data from a single source may arrive at results that differ from what is reported here. However, given the widely accepted utilization of this database, and given the difficulty in obtaining morphological characteristics for such a diverse family, we rely on published data for this study. Accordingly, we cross-referenced the values given by Jones et al. (2009) with ranges given by Nowak et al. (1994) for accuracy, and we did not include any species in the analyses for which these values were not available in the reference text or if there were discrepancies in the values. We included both body mass and forearm length in our analyses to avoid possible biases from each trait. Forearm length is related to flight ecology (Norberg and Rayner 1987; Blood and McFarlane 1988; Stockwell 2001; Adams 2008), and body mass can vary with individual health, gut volume, sex, and season (O'Farrell and Studier 1976; Piersma and Davidson 1991; Stockwell 2001; Storz et al. 2001; Nowak et al. 2004; Goodman et al. 2017), though both can be good body size indicators (Stockwell 2001; Storz et al. 2001; Willig et al. 2003; Meng et al. 2016).

Data Collection Methods

We measured the mesiodistal lengths and buccolingual widths of four teeth from the mandibular postcanine dentition (fourth premolar through third molar) of each specimen using Mitutoyo calipers and following standard protocols (e.g., Grieco et al. 2013). We restricted our study to adult bats, identified by the eruption of the third molars and canines (e.g., Giannini et al. 2006). Both males ($n = 62$) and females ($n = 39$) were included in the analyses. Each measurement was taken three times, once by each of three observers (MEZ, RRD, and SR). To assess interobserver error, the average difference between each pair of observer measurements for each specimen was divided by the sample mean for that metric to calculate measurement error as a percentage of the mean for the population. If the interobserver error was above 5%, all observers measured the specimen again, and a new average value was calculated. Final values are the average of the three repeated measurements provided the interobserver error was

Table 1   Pteropodid species sampled.*

Species	Male (*n*)	Female (*n*)	*N*	Average body mass (g)[a]	Average forearm length (mm)[a]	Specimen sampling location
Dobsonia minor	4	10	14	85.95	80.00	PNG: Central, East Sepik, and Madang Provinces
Dobsonia moluccensis	3	2	5	447.64	138.69	PNG: Morobe, New Ireland, and Western Highlands Provinces
Pteropus conspicillatus	15	4	19	760.71	174.06	Australia: Queensland PNG: Madang Province
Pteropus woodfordi	1	1	2	122.67	88.28	Solomon Islands: Guadalcanal Province
Pteropus yapensis	14	16	30	458.58	135.49	Micronesia: Yap Island
Rousettus amplexicaudatus	25	6	31	74.37	76.88	PNG: Madang Province
Total	**62**	**39**	**101**			

*Abbreviations as follows: *n* is sample size, *N* is total sample size, g is grams, PNG is Papua New Guinea. All specimens are held in the Museum of Vertebrate Zoology at the University of California, Berkeley

[a] Average body mass and forearm length data are from the PanTHERIA database (Jones et al. 2009, Appendix A). No molecular data were available for *Pteropus yapensis*. However, some researchers consider *P. yapensis* to be a subspecies of *P. mariannus* (Mickleburgh et al. 1992; Wiles 2005; Brown et al. 2011), with an estimated divergence time of 0.38 million years (Almeida et al. 2014), and so we used molecular and body size data for *P. mariannus* instead

below 5%. All dental metric data were size-corrected using geometric mean corrections to account for differences in body size across species. We assessed differences in metrics between the sexes before pooling specimens for analysis, because species in these genera are known to exhibit some sexually dimorphic traits.

As dental area is a well-recognized measure of dental variability in mammals (e.g., Hillson 2005), we also calculated dental area for our sample by multiplying mesiodistal length by buccolingual width, allowed by the approximately rectangular shape of the specimens' postcanine teeth (Fig. 2). We then performed a size-correction by calculating the geometric mean for dental area.

To assess variation in relative proportions of the postcanine dentition, we calculated the molar module component (MMC) and premolar/molar module (PMM) of each specimen as described by Hlusko et al. (2016). These ratios capture the morphological output of size-independent genetic mechanisms patterning the mammalian postcanine dentition. The MMC ratio is calculated as the mesiodistal length of the third molar (M_3) divided by the mesiodistal length of the first molar (M_1), and the PMM ratio is calculated as the mesiodistal length of the second molar (M_2) divided by the mesiodistal length of the fourth premolar (P_4) (Hlusko et al. 2016). As the MMC and PMM ratios were defined on the mandibular postcanine dentition of primates (P_4 through M_3), and as pteropodids have
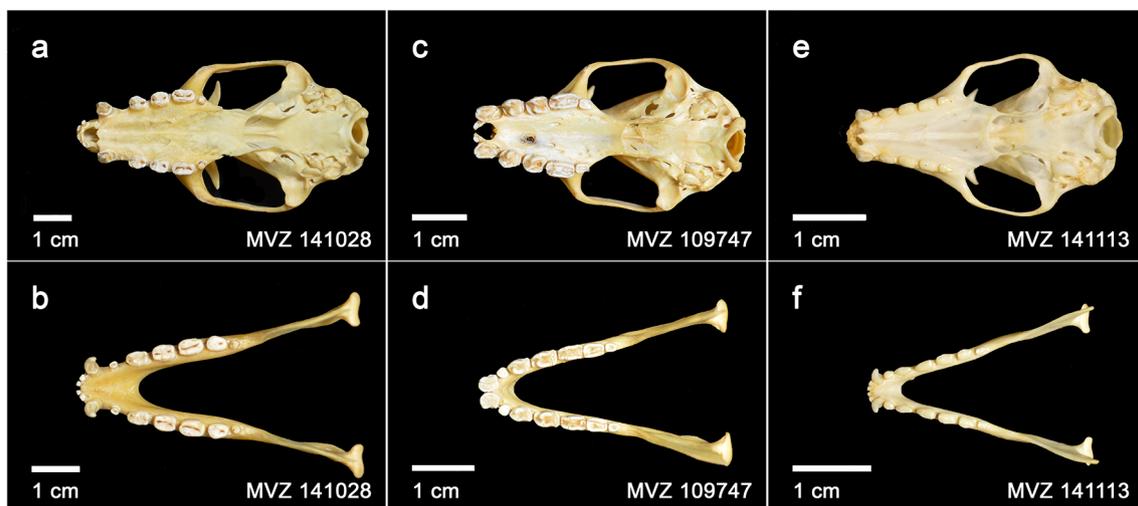
Fig. 2   Photographs showing variation in maxillary and mandibular dentition of *Pteropus conspicillatus* (**a** and **b**), *Dobsonia moluccensis* (**c** and **d**), and *Rousettus amplexicaudatus* (**e** and **f**)

different maxillary and mandibular dental formulas, with the M_3 only in the mandible (Giannini and Simmons 2007), we focused on mandibular measurements for this study. All raw dental data, calculated areas, and calculated MMC and PMM ratios are available in the full dataset (Supporting Information Appendix B).

Analytical Methods

All analytical methods were conducted using the R Statistical Environment v3.6.1 (R Core Team 2019). We calculated descriptive statistics for the sample using describeBy in *psych* (Revelle 2019) and visualized variation in dental metrics using boxplots with qplot in *ggplot2* (Wickham 2016). We statistically compared variation in dental metrics and proportions between sexes with parametric t-tests using default language in R (R Core Team 2019), and we compared species variation using ANOVA with the aov function (R Core Team 2019). Additionally, we ran a principal component analysis (PCA) including all geometric mean corrected dental length and width measurements with the prcomp in *psych* (Revelle 2019). As MMC and PMM are ratios, we visualized variation in these traits with a bivariate plot via *ggplot2* (Wickham 2016).

Phylogenetic Analyses

We generated a phylogeny of extant bats using published molecular data (Faurby and Svenning 2015), trimming the tree to only those species represented in our sample of pteropodids, plus one representative species for each extant bat family. The published molecular data (Faurby and Svenning 2015) is a merged supertree phylogeny generated using a heuristic-hierarchical Bayesian method compiled from sequences from multiple sources and augmented with GenBank data (one to eight nuclear genes [including CytB, 12S16S, APOB, DMP1, PRKC1, STAT5A, THY, TG, PRKC1, COI, PLCB4, PEPCK, vWf, 12S, 16 s, BRAC1, ND2, Usp9x, Chd1, Dby, Rag-1, and Rag-2] and one mitochondrial marker) and then validated against previously published molecular phylogenies at the inter- and intra-family levels (e.g., Jones et al. 2002; Meredith et al. 2011). All family-level placements were recovered with 100% posterior support, referring to post burn-in value (Faurby and Svenning 2015). The phylogenetic tree for this study was plotted in R (R Core Team 2019) using the read.tree and plot functions in the *ape* package (Paradis et al. 2004).

To evaluate body size changes in Chiroptera, and in Pteropodidae specifically, we generated an ancestral state reconstruction of body mass and forearm length across our phylogeny of extant bats using contMap and fastAnc in *phytools* (Revell 2012). To further investigate the relationship between dental morphology and body size in megabats, we ran a series

of phylogenetic analyses. First, we statistically compared body mass and forearm length with geometric mean size-corrected dental metric data (length and width), two-dimensional dental data (dental area), and the MMC and PMM ratios using phylogenetic independent contrasts. Phylogenetic independent contrasts compare phenotypes while taking the structure of the phylogenetic tree into account (Rickleffs and Starck 1996). We also estimated the phylogenetic signal of the dental metric data and the MMC and PMM traits with Pagel's lambda (λ) using fitContinuous in *geiger* (Harmon et al. 2019). A Pagel's lambda score approaching 1 indicates conserved phylogenetic signal, while a lambda score approaching 0 indicates no phylogenetic signal in the trait (Pagel 1999).

Results

Descriptive statistics capture the variation in dental linear metrics, dental area, and dental proportions between pteropodid species sampled here (Table 2). Average tooth lengths, widths, and areas are largest in *Pteropus conspicillatus* and smallest in *Pteropus woodfordi* (Table 2, Fig. 3). We observed the most variation in dental metrics in *Dobsonia moluccensis* (Table 2, Fig. 3), which may be further investigated with a larger sample size. We find no significant sex differences in dental metrics or ratios except in the length of the P_4 of *Rousettus amplexicaudatus* (t-test, $p < 0.05$), a known sexually dimorphic species (Nowak et al. 1994). As such, data for males and females were pooled for all statistical analyses to increase sample sizes.

A principal component analysis including dental linear metric data and dental area discriminates most of the species with some overlap in *Dobsonia moluccensis* and *Pteropus yapensis*, both medium-sized fruit bats (Fig. 4). PC1 captures body size variation, with the largest species, *Pteropus conspicillatus,* plotting in positive PC1 space, and the smaller species, *Rousettus amplexicaudatus, Dobsonia minor*, and *Pteropus woodfordi,* plotting in negative PC1 space.

A bivariate plot comparing MMC and PMM demonstrates a different pattern of morphological variation than is seen when comparing species using dental linear metrics (Fig. 5). There is good taxonomic discrimination of genera using these two ratios, particularly along the axis of MMC. The MMC ratio is significantly different between all genera (ANOVA, $p < 0.05$). There is more overlap in values of PMM, and values for this trait are significantly different only when comparing *Dobsonia minor* to the other pteropodid species (ANOVA, $p < 0.05$). Although variation in dental metrics can be attributed to variation in body size, dental proportions (MMC and PMM) cluster by phylogenetic relatedness rather than body size (Fig. 5).

Table 2 Descriptive statistics for the dental linear metrics (length and width), dental area, and the MMC and PMM ratios, by species.*

Species	Trait	Mean	SD	Range	Skew	Kurtosis	SE
Dobsonia minor (n = 14)	P_4L	2.75	0.13	0.51	−0.58	−0.03	0.04
	M_1L	2.66	0.18	0.65	−1.11	0.41	0.05
	M_2L	2.02	0.10	0.35	0.06	−1.16	0.03
	M_3L	1.18	0.08	0.24	−0.06	−1.58	0.02
	P_4W	1.83	0.14	0.45	−0.77	−0.56	0.04
	M_1W	1.52	0.08	0.24	−0.93	−0.76	0.02
	M_2W	1.37	0.07	0.27	−0.21	−0.74	0.02
	M_3W	0.94	0.08	0.33	−1.52	2.04	0.02
	P_4A	5.04	0.52	1.86	−0.97	−0.06	0.14
	M_1A	4.07	0.46	1.49	−1.04	−0.25	0.12
	M_2A	2.77	0.23	0.87	−0.19	−0.40	0.06
	M_3A	1.11	0.15	0.52	−0.48	−0.84	0.04
	MMC	0.44	0.03	0.12	0.58	0.41	0.01
	PMM	0.73	0.04	0.13	−0.28	−1.04	0.01
Dobsonia moluccensis (n = 5)	P_4L	4.34	0.52	1.11	0.25	−2.21	0.23
	M_1L	4.24	0.58	1.45	0.52	−1.66	0.26
	M_2L	3.60	0.42	0.91	0.37	−2.08	0.19
	M_3L	1.96	0.39	0.93	0.17	−2.07	0.18
	P_4W	2.72	0.37	0.83	0.24	−2.07	0.17
	M_1W	2.49	0.38	0.85	0.25	−2.12	0.17
	M_2W	2.41	0.32	0.76	0.45	−1.80	0.14
	M_3W	1.56	0.23	0.61	0.59	−1.42	0.10
	P_4A	11.97	3.05	6.74	0.29	−2.14	1.36
	M_1A	10.70	3.12	7.20	0.43	−1.88	1.40
	M_2A	8.77	2.19	4.93	0.46	−1.89	0.98
	M_3A	3.12	1.08	2.72	0.41	−1.76	0.48
	MMC	0.46	0.05	0.12	−0.35	−1.84	0.02
	PMM	0.83	0.03	0.06	0.26	−1.83	0.01
Pteropus conspicillatus (n = 19)	P_4L	4.84	0.21	0.78	−0.73	−0.46	0.05
	M_1L	5.14	0.24	0.96	−0.50	−0.36	0.06
	M_2L	3.99	0.27	1.00	−0.83	−0.08	0.06
	M_3L	2.01	0.28	1.07	0.41	−0.60	0.06
	P_4W	3.52	0.15	0.54	0.33	−0.81	0.04
	M_1W	3.46	0.16	0.62	0.47	−0.78	0.04
	M_2W	3.17	0.17	0.71	−0.44	−0.26	0.04
	M_3W	1.88	0.18	0.71	−0.29	−0.66	0.04
	P_4A	17.04	1.25	4.74	−0.08	−0.84	0.29
	M_1A	17.76	1.43	6.10	−0.22	−0.42	0.33
	M_2A	12.65	1.37	5.48	−0.83	0.09	0.31
	M_3A	3.81	0.84	3.17	0.27	−0.76	0.19
	MMC	0.39	0.05	0.20	0.37	−0.35	0.01
	PMM	0.82	0.04	0.12	0.03	−1.31	0.01
Pteropus woodfordi (n = 2)	P_4L	2.20	0.05	0.08	0.00	−2.75	0.04
	M_1L	2.23	0.04	0.06	0.00	−2.75	0.03
	M_2L	1.68	0.03	0.04	0.00	−2.75	0.02
	M_3L	0.98	0.00	0.00	0.00	−2.75	0.00
	P_4W	1.33	0.08	0.12	0.00	−2.75	0.06
	M_1W	1.37	0.10	0.14	0.00	−2.75	0.07
	M_2W	1.31	0.04	0.05	0.00	−2.75	0.03

Table 2 (continued)

Species	Trait	Mean	SD	Range	Skew	Kurtosis	SE
	M_3W	0.82	0.01	0.01	0.00	−2.75	0.01
	P_4A	2.93	0.26	0.36	0.00	−2.75	0.18
	M_1A	3.06	0.28	0.40	0.00	−2.75	0.20
	M_2A	2.20	0.03	0.04	0.00	−2.75	0.02
	M_3A	0.81	0.01	0.01	0.00	−2.75	0.01
	MMC	0.44	0.01	0.01	0.00	−2.75	0.01
	PMM	0.77	0.03	0.05	0.00	−2.75	0.02
Pteropus yapensis ($n = 30$)	P_4L	3.87	0.22	0.80	0.21	−1.00	0.04
	M_1L	4.13	0.20	0.82	0.35	−0.40	0.04
	M_2L	3.10	0.19	0.73	0.35	−0.60	0.03
	M_3L	1.51	0.20	0.81	−0.40	−0.52	0.04
	P_4W	2.55	0.11	0.40	−0.22	−0.83	0.02
	M_1W	2.41	0.07	0.31	−0.63	0.04	0.01
	M_2W	2.24	0.08	0.35	−0.11	−0.62	0.02
	M_3W	1.38	0.19	0.86	−1.16	1.41	0.03
	P_4A	9.87	0.78	2.91	−0.20	−0.98	0.14
	M_1A	9.96	0.67	2.82	−0.23	−0.55	0.12
	M_2A	6.96	0.61	2.38	0.21	−0.69	0.11
	M_3A	2.13	0.52	2.29	−0.37	−0.10	0.10
	MMC	0.37	0.04	0.17	−0.24	−0.39	0.01
	PMM	0.80	0.04	0.17	−0.22	−0.24	0.01
Rousettus amplexicaudatus ($n = 31$)	P_4L	2.40	0.08	0.29	−0.19	−0.97	0.01
	M_1L	2.37	0.09	0.34	0.26	−1.22	0.02
	M_2L	1.98	0.08	0.30	−0.32	−0.93	0.01
	M_3L	1.42	0.10	0.37	−0.19	−1.06	0.02
	P_4W	1.45	0.08	0.30	−0.14	−1.13	0.01
	M_1W	1.51	0.09	0.33	−0.28	−1.01	0.02
	M_2W	1.42	0.07	0.27	−0.04	−0.62	0.01
	M_3W	1.00	0.07	0.25	0.51	−0.68	0.01
	P_4A	3.47	0.27	0.96	−0.18	−1.00	0.05
	M_1A	3.57	0.32	1.21	0.03	−1.14	0.06
	M_2A	2.82	0.22	0.80	−0.27	−1.02	0.04
	M_3A	1.42	0.18	0.63	0.26	−0.96	0.03
	MMC	0.60	0.04	0.16	−0.18	−0.77	0.01
	PMM	0.83	0.04	0.15	−0.28	−0.63	0.01

*Abbreviations as follows: P is premolar, M is molar, L is length, W is width, A is area; subscript number denotes mandibular tooth position, e.g., P_4L is mandibular fourth premolar length. MMC is molar module component, PMM is premolar/molar module. SD is standard deviation, SE is standard error

We compared average body mass and forearm length of each species to metrics of tooth length, width, and area, as well as the MMC and PMM ratios, using phylogenetic independent contrasts (Table 3). All dental metrics are significantly correlated with body mass independent of phylogenetic relatedness. The PMM ratio is also significantly correlated with body mass ($p = 0.035$) and forearm length ($p = 0.019$). When taking phylogenetic relatedness into account, there is no significant relationship between variation in the MMC ratio and body mass ($p = 0.806$) or forearm length ($p = 0.826$) in megabats,

consistent with what has been previously observed in primates (Hlusko et al. 2016) and other mammals (Monson et al. 2019).

Our estimate of Pagel's lambda returns evidence of a conserved phylogenetic signal in MMC ($\lambda = 1.00$, $p < 0.001$), but no significant phylogenetic signal in PMM or any of the dental metrics (length, width, or area). Additionally, we find no phylogenetic signal in body size for the pteropodid sample ($\lambda = 0.00$), and very low phylogenetic signal in body size across bats more broadly ($\lambda = 0.276$), supporting multiple changes in body size across lineages in chiropteran evolution.
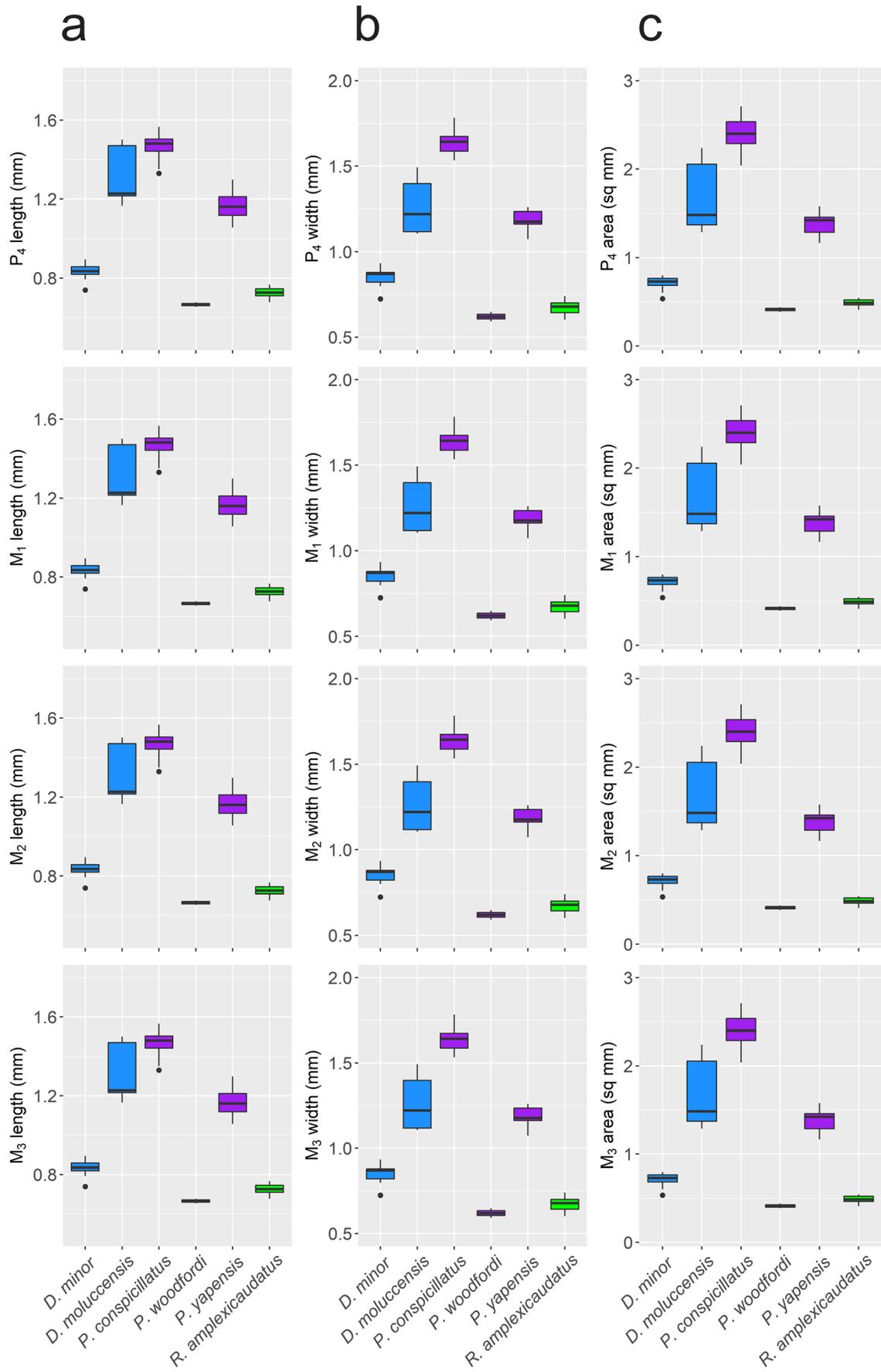
Discussion

One of the most defining characteristics of megabats is their generally large size compared to microbats (Nowak et al. 1994; Kirsch et al. 1995; Teeling et al. 2005; Agnarsson et al. 2011; Almeida et al. 2011; Giannini et al. 2012). This dramatic increase in body size is coupled with a diverse range of frugivory and nectarivory and the loss of laryngeal echolocation. We undertook a nuanced analysis of postcanine dental variation among pteropodid taxa to enhance our understanding of the dental variation involved with this ecological and dietary adaptive radiation (Freeman 1995, 1998; Phillips 2000; Aguirre et al. 2003; Dumont 2004). We analyzed three types of dental data, as the combination offers more insight than any one type of measurement in isolation: linear metrics, two-dimensional crown area, and ratios that reflect the underlying genetic architecture. Our analyses yield three main observations discussed in more detail below: 1) taxa are distinct in their dental metrics and proportions; 2) tooth size variation is associated with body size independent of phylogeny; and 3) variation in tooth proportions (MMC) is significantly associated with phylogeny.

Dental metrics are relatively unique between taxa (Figs. 3-4) with no clear relationship to phylogeny. Only one dental metric was found to be sexually dimorphic in one species. We found this result to be surprising, as sexual dimorphism is common in many pteropodid species. Typically, pteropodid males have a higher average body mass than females (Rousettus: Nowak et al. 1994; Goodman et al. 2017,

Fig. 5 Bivariate plot comparing MMC and PMM in Pteropodidae. See legend in figure for species information. These dental ratios discriminate specimens taxonomically; compare to Fig. 4, and see text for details

Pteropus: Nowak et al. 1994; McNab and Armstrong 2001; Welbergen 2010). In some species, males also have longer forearms than females (Rousettus: Goodman et al. 2017, Pteropus: Welbergen 2010). In one pteropodid genus, male and female-biased sexual dimorphism in body mass occurs at different latitudes, though species with smaller ranges likely do not exhibit this pattern (Storz et al. 2001). Fewer generalizations can be made about sexual dimorphism of pteropodid dental morphology. In several *Pteropus* species, males have larger lower canines than females (Giannini et al. 2006; Rahman and Abdullah 2010), and one *Rousettus* species is

Fig. 4 Principal component analysis of postcanine dental metrics in pteropodids. Measurements included are: mesiodistal lengths (fourth mandibular premolar, and first through third mandibular molars), and buccolingual widths (fourth mandibular premolar, and first through third mandibular molars). All measurements were geometric mean size-corrected prior to analysis. PC1 captures body size; see text for details

Table 3 Results of the phylogenetic independent contrasts comparing dental data with body mass and forearm length.*

Metric	Tooth	Body Mass (R^2)	Body Mass (*p*-value)	Forearm Length (R^2)	Forearm Length (*p*-value)
Length	P_4L	0.967	**0.000**	0.987	**0.000**
	M_1L	0.973	**0.000**	0.984	**0.000**
	M_2L	0.958	**0.001**	0.988	**0.000**
	M_3L	0.947	**0.001**	0.966	**0.000**
Width	P_4W	0.968	**0.000**	0.921	**0.002**
	M_1W	0.980	**0.000**	0.932	**0.001**
	M_2W	0.997	**0.000**	0.975	**0.000**
	M_3W	0.993	**0.000**	0.982	**0.000**
Area	P_4A	0.984	**0.000**	0.945	**0.001**
	M_1A	0.968	**0.001**	0.912	**0.002**
	M_2A	0.991	**0.000**	0.962	**0.000**
	M_3A	0.981	**0.000**	0.969	**0.000**
MMC	M_3L/M_1L	−0.229	0.806	−0.233	0.826
PMM	M_2L/P_4L	0.640	**0.035**	0.727	**0.019**

*Abbreviations as follows: P is premolar, M is molar, L is length, W is width, A is area; subscript number denotes mandibular tooth position, e.g., P_4L is mandibular fourth premolar length. R^2 is coefficient of determination. MMC is molar-molar module, PMM is premolar/molar module. Bolded *p*-values are significant

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sexually dimorphic in upper toothrow length (Benda et al. 2012). Although pteropodids often sexually differ by body mass, these selective pressures may not act similarly on the postcanine dentition. Further analysis including larger sample sizes, more taxonomic diversity, and specific dietary knowledge may reveal more clear relationships between sex, size, and dental morphology.

Tooth size has long been recognized as a proxy for body size (Gould 1975; Gingerich 1977; Goldstein et al. 1978; Gingerich and Schoeninger 1979; Creighton 1980; Gingerich et al. 1982; Caumul and Polly 2005). The association we observed between pteropodid body size (as captured by body mass and forearm length) and tooth size (as captured by linear metric and two-dimensional area) is assumed to result from shared genetic effects as has been reported extensively in other mammals through quantitative genetic analyses (e.g., Hlusko et al. 2006), molecular studies (e.g., Caumul and Polly 2005), and evolutionary patterns (e.g., Gould 1975; Gingerich 1977; Goldstein et al. 1978; Gingerich and Schoeninger 1979; Creighton 1980; Gingerich et al. 1982; Caumul and Polly 2005). Our ancestral state reconstruction (Fig. 6) suggests that the last common ancestor of extant pteropodids was a moderately-sized bat, and that significant body size increases evolved over the last 26 million years, consistent with what has been previously reported (Kirsch et al. 1995; Teeling et al. 2005; Agnarsson et al. 2011; Arévalo et al. 2020).

The linear and two-dimensional assessments of tooth crown size may be capturing evidence of selection for an increase in body size due to frugivory on islands and other tropical ecosystems, where abundant fruit trees are a good source of both food and shelter. Researchers have previously observed a positive correlation between body size and ingested fruit size in megabats, suggesting that increased body size allowed pteropodids to exploit novel food resources on islands (Fleming et al. 1987; Campbell et al. 2007). Over half of the extant pteropodid species live on islands, and island habitats likely had a strong influence on the evolution of pteropodid body size (Cardillo and Meijaard 2010; Raia et al. 2010). Smaller mammals do tend towards increasing body size on islands, an ecological effect of decreased predation and increased food resources (Case 1978; Heaney 1978; Lawlor 1982; Palkovacs 2003; Lomolino 2005).

Food resources may be the critical factor in the evolution of larger body size in the pteropodids. Fruit hardness is correlated with variation in craniodental morphology in some bats (Dumont 1997, 2004, 2007; Freeman 1998; Aguirre et al. 2003). Given that greater bite force is needed to consume harder-skinned fruits, and given the associated increase in bite force that comes with a larger body size, some megabats may have experienced selection for increased body size that may have enabled utilization of larger, hard-skinned fruits (Aguirre et al. 2002, 2003, 2004; Dumont 2004). Some smaller
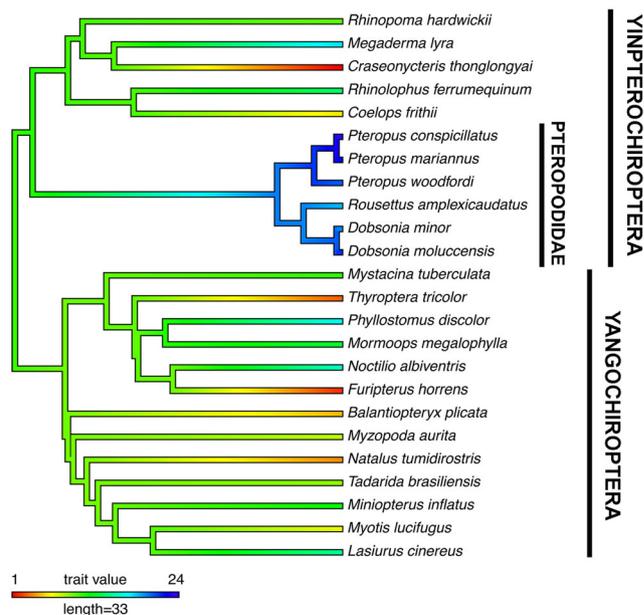
Fig. 6 Ancestral state reconstruction of scaled body size in bats. Average body mass and forearm length are from the PanTHERIA database (Jones et al. 2009; Appendix A) and cross-referenced with Nowak et al. (1994). Note large body size derived in pteropodids. No molecular data were available for *Pteropus yapensis*. However, some researchers consider *P. yapensis* to be a subspecies of *P. mariannus* (Mickleburgh et al. 1992; Wiles 2005; Brown et al. 2011), with an estimated divergence time of 0.38 million years (Almeida et al. 2014), and so we used molecular and body size data for *P. mariannus* instead

pteropodids like *Dobsonia minor*, however, are able to overcome difficulty of eating hard-skinned fruits by changing feeding strategies, for example, by biting deeply and bilaterally (Bonaccorso et al. 2002; Dumont and O'Neal 2004; Walker et al. 2004).

While there is a strong correlation between tooth size and body size, mammalian dentitions clearly reflect more than just the evolution of body size. Mammalian heterodonty captures a dramatic range of variation in the relative sizes of teeth along the tooth row in addition to a vast array of variation in the third dimension. To better capture variation in relative tooth sizes, the MMC and PMM ratios were developed through an evolutionary quantitative genetic analysis across African and Asian primates (Hlusko et al. 2016). These two traits provide an assessment of postcanine dental variation that reflects the genetic mechanisms underlying variation in the relative sizes of teeth independent of the genetic influences on body size (Hlusko et al. 2016). Given the similarities between mouse and baboon dental genetic architectures (Hlusko et al. 2011), these genetic mechanisms are likely conserved across mammals (Monson et al. 2019) and therefore, we include them here to test their applicability to bats.

Our analyses of dental morphology, body size, and phylogenetics demonstrate that 1) pteropodid species can be distinguished by dental morphology, and 2) in sharp contrast to the strong relationship between tooth size and body size, 3)

variation in the MMC among pteropodids reflects phylogenetic relatedness rather than body size. In accordance with our predictions, these results indicate that MMC is a more ideal morphological trait for discerning phylogeny compared to linear tooth size measurements. Additionally, MMC may also represent a mechanism through which the evolution of dietary specialization can be better understood.

Our results show that *Pteropus – Dobsonia – Rousettus* form a continuum of MMC values (Fig. 5). Selection on the nectarivory or omnivory phenotypes may include changes in dental proportions that lead to a relatively longer third molar and higher MMC ratio. Focusing on the higher end of the ratio first, Wilson (1973) calculated dietary proportions of bats and found that nectar comprises around half of the *Rousettus* diet and much less in the diets of *Dobsonia* and *Pteropus* (20% and 10% of the diet, respectively), with the remaining diet consisting of fruits (Wilson 1973). The diet of *Rousettus amplexicaudatus* includes flower nectar and fruit juices, and this species is commonly considered to be frugo-nectarivorous or omnivorous (Walker et al. 2004; Stewart et al. 2014). While these bats may accidentally consume insects on flowers or fruit (Dumont 2003), there is evidence that some *Rousettus amplexicaudatus* individuals eat insects intentionally, further indicating an omnivorous phenotype (Barclay et al. 2006). Within our sample, *Rousettus amplexicaudatus* is more omnivorous than the other species and has craniodental characteristics more typical of nectarivorous bats, such as an elongated rostrum and palate (Fig. 2, Freeman 1988; Kitchener et al. 1990; Freeman 1995; Birt et al. 1997; Kirsch and Lapointe 1997; Freeman 1998). This nectarivory-like anatomy may underlie *Rousettus amplexicaudatus*' position at the high end of the MMC spectrum.

It is interesting to note that the association of a higher MMC value with a longer rostrum in *Rousettus* is also observed in primates: the long rostrums of the papionins are associated with relatively higher MMC values (and relatively longer third molars, Hlusko et al. 2016). An alternative, possibly interrelated, phenomenon to keep in mind is that *Rousettus amplexicaudatus* is one of very few bat species that can echolocate using tongue clicks (Griffin et al. 1958; Novick 1958; Nowak et al. 1994; Funakoshi et al. 1995; Holland et al. 2004; Jones and Teeling 2006; Yovel et al. 2011; Schoeman and Goodman 2012; Nesi et al. 2013; Wilson 2015); this behavior may have implications for craniodental morphology. Future studies on the relationship between craniodental variation, diet, and lingual echolocation in *Rousettus* and other preferentially nectarivorous bat species may further clarify the differences in dental proportions seen in this genus relative to other megabats.

Both *Dobsonia* species and *Pteropus woodfordi* occupy the middle of the MMC spectrum. There is little known about the specific diet of *Pteropus woodfordi*; more detailed information on the diet and a larger sample size of *Pteropus*

woodfordi may clarify our results. Bats in the genus *Dobsonia* eat a variety of fruits, particularly hard-skinned figs (Bonaccorso et al. 2002; Walker et al. 2004). In particular, *Dobsonia minor* bats preferentially eat hard-skinned figs, which requires large bite force (Bonaccorso et al. 2002; Dumont and O'Neal 2004).

Fig is also a preferred fruit for *Pteropus conspicillatus*, though they also consume other fruits, flowers, and nectar (Dumont 2003, 2004; Parsons et al. 2007). With 60 recognized species (Walker et al. 2004; Simmons 2005b), bats of the genus *Pteropus* have a variety of dietary preferences, with some species preferentially nectarivorous (Southerton et al. 2004). In general, *Pteropus* bats eat mostly fruit juice and pulp and, depending on availability, will occasionally eat leaves and flowers (Richards 1990; Pierson and Rainey 1992; Wiles and Fujita 1992; Walker et al. 2004; Parsons et al. 2007). While *Pteropus conspicillatus* ascribes to this pattern, as fruits comprise approximately 80% of their diet, *Pteropus yapensis* is more generalist (Richards 1990). *Pteropus yapensis* can exclusively be found on the island of Yap, a range of only 100 km^2 (Falanruw 1988). As such, these bats eat a wide variety of fruits and flowers, preferring breadfruit, and other foliage when their preferred foods are in short supply (Falanruw 1988; Wiles and Fujita 1992). The low end of the MMC spectrum is occupied by these more generalist taxa, while more frugivorous species occupy middle MMC ranges and nectarivorous-omnivorous bats occupy the high end of the MMC spectrum. Including species with more taxonomic and dietary variation in our analyses will increase the robustness of our findings and further disentangle the relationship between diet, phylogeny, and MMC.

In contrast to MMC, we find that the PMM ratio is more variable within pteropodid species than MMC and shows an association with body size, though it is weaker than we found for the linear or two-dimensional metrics. The weaker but statistically significant association between PMM and body size may be related to sexual dimorphism. Previous work has shown that some pteropodid taxa have sexually dimorphic skeletal and craniodental morphology (Giannini et al. 2006; Campbell et al. 2007; Rahman and Abdullah 2010; Benda et al. 2012; Maryanto et al. 2012). As sexual dimorphism in both body size and cranial morphology has been demonstrated in species of *Rousettus* (Nowak et al. 1994; Benda et al. 2012; Goodman et al. 2017), and we observed sexual dimorphism in the P$_4$ of *Rousettus amplexicaudatus*, the association between this premolar-molar ratio and body size may be in part due to sexual dimorphism.

In conclusion, we note that megabats are vital ecosystem contributors that serve as potential disease vectors and have impacts on pollination and agriculture (e.g., Breed et al. 2010; Luis et al. 2013; Aziz et al. 2015; Olival 2016; Vincenot et al. 2017). Due to the critical conservation status of many

megabats (Marshall 1983; Fujita and Tuttle 1991; Korine et al. 1999; Brown et al. 2011), many species may be exclusively represented by museum collections and in zoos if hunting and habitat degradation continues, or with the ongoing effects of climate change (Fujita and Tuttle 1991; Welbergen et al. 2008; Daniel et al. 2016; Vincenot et al. 2017). Therefore, investigation of the dental variation captured in museum skeletal collections will be essential to advancing our understanding of the evolution of Chiroptera. Our research demonstrates that different means of phenotypic assessment can yield different insights. We found that linear assessments of crown size largely reflect variation in body size, a trait known to be highly evolvable (e.g., Marshall and Corruccini 1978; Creighton 1980; Lister 1989). In comparison, MMC is more phylogenetically conserved and may elucidate deeper evolutionary trends in dietary divergence. This combination of different approaches for characterizing dental variation provides an opportunity to identify and refine our understanding of the selective pressures on the Pteropodidae radiation by expanding what can be learned from museum skeletal collections.

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