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Patterns of diversity in cranial shape among plant-visiting bats

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Adaptations to a plant-based diet have evolved in bats on two occasions — once in the Old World family Pteropodidae and again within the New World family Phyllostomidae. Although the skulls of all plant-visiting bats exhibit adaptations for relatively large eyes, enlarged brains, and reduced molar complexity, the skulls of bats from the two families look very different. The goals of this study are to pinpoint the fundamental differences in the cranial shape between pteropodids and plant-visiting phyllostomids and to investigate patterns of diversity in cranial shape within each lineage. Analyses are based on 19 size adjusted, linear variables collected from 335 specimens that represent 71% of pteropodid and 45% of plant-visiting phyllostomid genera. Results of a stepwise discriminant function analysis indicate that differences in cranial shape between pteropodids and plant-visiting phyllostomids involve general aspects of relative braincase width, palate width and coronoid process height. Pteropodids have relatively narrow skulls and palates, and dentaries with tall coronoid processes, while the opposite is true of phyllostomids. Principal components analysis and an investigation of coefficients of variation reveal a high level of variation among the skulls of plant-visiting phyllostomids while cranial architecture among pteropodids is more conservative. This study documents patterns of morphological diversity in the skulls of plant-visiting bats. Several potential ecological and biomechanical mechanisms underlying these patterns are discussed.

Key words: Pteropodidae, Phyllostomidae, plant-visiting, cranial shape, diversity, constraint

INTRODUCTION

The independent origins of associations between morphology and ecology are often viewed as evidence of adaptation (e.g., Larson and Losos, 1996). There are many examples of morphological and ecological convergence among bats that are linked to diet. One of the most widely cited instances of trophic convergence is the independent evolution of plant-visiting in the families Pteropodidae (Old World fruit bats) and Phyllostomidae (New World leaf-nosed bats) (see review in Dumont, 2003). Both families contain species that rely on fruit and/or nectar as a primary food source during at least some portion of the year. Both groups also exhibit similar levels of generic diversity in plant-visiting taxa. All 42 genera of pteropodids rely on plant resources as their primary source of food (Mickleburgh *et al*., 1992; Koopman, 1993). The diets of 40 genera of phyllostomids focus on plant resources; the remaining 17 genera feed on insects, small vertebrates, or blood (Swanepoel and Genoways, 1983; Ferrarezzi and Gimenez, 1996; Wetterer *et al*., 2000).

The dietary adaptations of mammals are commonly reflected in the morphology of

their skulls, and many studies of bats have documented associations between cranial morphology and diets of insects, fruit, nectar, and small vertebrates (Freeman, 1981, 1984, 1988, 1995; Dumont, 1997; Van Cakenberghe *et al*., 2002). Cranial shape among fruit-eating bats is quite variable (Freeman, 1988; Dumont, 1997), probably because fruits exhibit a wide range of physical properties (e.g., Ungar, 1995; Strait and Overdorff, 1996; Aguirre *et al*., 2003; Dumont, 2003). Most nectar-feeding bats have elongated rostra and tongues that increase the efficiency of nectar extraction (Nicolay and Dumont, 2000; Nicolay, 2001; Winter and von Helverson, 2003). However, in comparison to insectivorous bats, all plant-visiting bats have relatively large eyes, large brains, and reduced molar complexity (e.g., Hill and Smith, 1984; Neuweiler, 2000; Hutcheon *et al*., 2002; Phillips, 2003). Plant-visiting bats from both families also rely on olfactory cues to locate ripe fruit (e.g., Rieger and Jakob, 1988; Laska, 1990; Acharya *et al*., 1998; Luft *et al*., 2003), a behavior that is associated with their relatively large olfactory bulbs (Hutcheon *et al*., 2002; Reep and Bhatnagar, 2003). Despite fundamental similarities among bats that feed on plant resources, the skulls of pteropodids and plant-visiting phyllostomids differ in obvious ways.

Perhaps the most striking difference in skull morphology between the two lineages of plant-visiting bats is in the upper face. Relatively large and well-buttressed orbits are characteristic of the skulls of pteropodids. This reflects their relatively large eyes and reliance on vision during nocturnal foraging. In contrast, the skulls of plant-visiting phyllostomids resemble those of echolocating insectivorous bats in having orbits with poorly-defined margins. Phyllostomids emit echolocation sounds through their noses and plant-visiting species use both echolocation and vision during foraging (Kalko and Condon, 1998; Thies *et al*., 1998). While the skulls of pteropodids are often viewed as unspecialized and relatively invariant across species (e.g., Miller, 1907; Fleming, 1993), plant-visiting phyllostomids are well-known for spectacular extremes in cranial shape (e.g., Freeman, 1988, 2000).

Despite the apparent differences in cranial shape between pteropodids and plant-visiting phyllostomids, no study has pinpointed the elements of skull shape that reliably distinguish between the two lineages. Similarly, no one has either documented variability in skull form within each group or compared the range of variation between them. Accomplishing these analyses can set the stage for investigations into the factors that have influenced the evolution of diversity in cranial shape among plant-visiting bats. For example, significant overlap in the range of skull form between the two lineages would suggest that skull form has evolved along similar pathways to meet the mechanical demands of ingesting plant resources. Alternatively, the presence of unique subsets of conserved and variable elements of skull shape within each group would suggest that different selective pressures and/or constraints on skull form have influenced the evolution of phytophagy within the two groups.

The goal of this study is to investigate two specific questions about skull shape in plant-visiting bats. First, how does the shape of the skull differ between pteropodids and plant-visiting phyllostomids? Discriminant function analysis is applied to size adjusted linear measurements to identify significant, reliable differences in skull shape between the two groups. The second question is; within each lineage, which regions of the skull are conserved and which vary among species? Two different approaches are used to address this question. Principal components

analysis is used to generate a 'snapshot' of variation across a combined sample of pteropodid and plant-visiting phyllostomid species and offers insights into the differences between the two groups. To evaluate variation in each lineage independently, sample statistics for coefficients of variation for each skull shape variable are compared between groups to highlight differences in the occurrence and magnitudes of variation.

Materials and Methods

I collected 19 linear measurements from the skulls and dentaries of 335 plant-visiting bats (Fig. 1, Appendix). These measurements were selected to reflect both overall skull dimensions and more limited anatomical regions and have been used successfully to describe variation in cranial shape in several other clades of mammals (Dumont, 1997, 2000). The data set contains individuals from 18 species of plant-visiting phyllostomids, and 30 species of pteropodids. The sample covers 71% of pteropodid and 45% of plant-visiting phyllostomid genera. Each species is

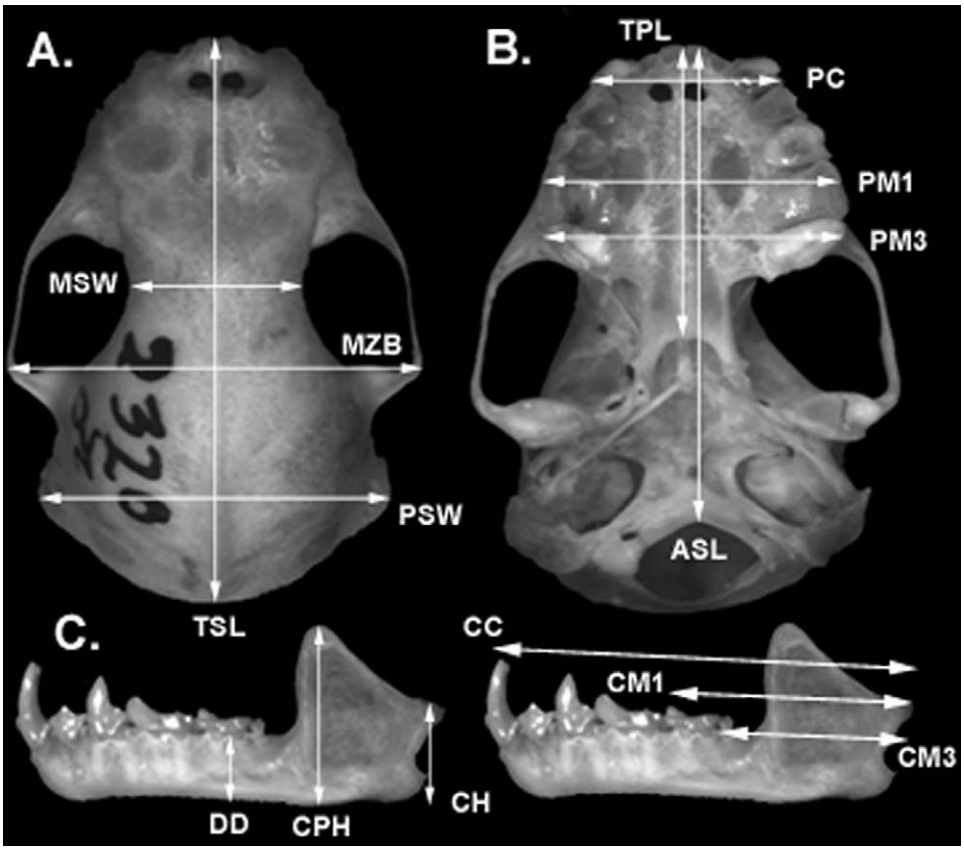

Fig. 1. Linear measurements included in this study illustrated using *Artibeus jamaicensis*. A. Dorsal view of the skull illustrating minimum skull width (MSW), maximum zygomatic breadth (MZB), posterior skull width (PSW), total skull length (TSL). B. Ventral view of the skull illustrating total palate length (TPL), palate width at canine (PC), palate width at m1 (PM1), palate width at m3 (PM3), anterior skull length (ASL). C. Lateral view of the dentary illustrating dentary depth under m1 (DD), coronoid process height (CPH), condyle height (CH), condyle to canine length [CC; in this case, is equal to total dentary length (TDL)], condyle to m1 length (CM1), and condyle to m3 length (CM3). The measurements skull height (SH, foramen magnum to vertex measured perpendicular to the plane of the upper molar teeth), condyle length (CL, greatest antero-posterior length), and condyle width (CW, greatest medio-lateral width) are not illustrated

represented by an average of seven individuals (SD = 3.7, range = 2–16). With the exceptions of *Ardops nichollsi* (males only) and *Phylloderma stenops* (females only), samples for all species contain both males and females. Because osteological specimens occasionally exhibit minor damage, 25 of the 6,365 possible measurements (0.4%) were missing from the data set. Rather than deleting individuals with single missing data points from analysis, the occasional missing measurement was replaced with the mean value derived from the other individuals of the same species and sex. Samples sizes for each species are not equal. To generate a dataset that weights each species equally, each of the 19 variables for each species was represented by either the mean of all individual values (when male and female sample sizes were equal) or the midpoint of male and female mean values (when sample sizes for males and females were unequal). The sexes were weighted equally due to the presence of dimorphism in epomophorines (Nowak, 1994) and some phyllostomids (Nicolay, 2001).

Because the species included in this study cover a wide range of body sizes, it was important to generate size-adjusted variables. I accomplished this using a geometric mean procedure. Using this technique, raw values for each individual were divided by the geometric mean of all measurements from that individual and then transformed using natural logarithms (Darroch and Mosimann, 1985; Falsetti *et al*., 1993; Jungers *et al*., 1995). Although this method does not adjust for allometric components of size, it creates individually size-adjusted shape variables that are independent of the composition of the data set.

Overall differences between the skulls of pteropodids and plant-visiting phyllostomids were investigated using stepwise discriminant function analysis (SPSS, version 10.0). This method enters variables into the analysis in order of their ability to discriminate between the two groups. Only variables that significantly discriminate between the two groups at the $P = 0.1$ level (based on analysis of variance) were included. With the addition of subsequent variables, the significance of each included variable is retested. A variable is removed from the analysis if the significance of its contribution to discriminating between the two groups rises above $P = 0.15$. The completed discriminant function analysis identifies a combination of variables and coefficients that differentiate pteropodids from plant-visiting phyllostomids. The utility of the equation is evaluated by assessing its ability to correctly predict the family membership of new species. In this case, this was accomplished using a jackknife cross validation procedure that sequentially removes each species from the analysis and then classifies it based on a discriminant function derived from all the other species in the analysis. This procedure reduces the bias toward success that is inherent in classifying cases using a discriminant function derived from those same cases (Tabachnick and Fidell, 1996).

To generate an overall picture of patterns of variation in pteropodids and plant-visiting phyllostomids simultaneously, all species and variables were entered into a principal components analysis (SPSS, version 10.0). This analysis highlights combinations of morphological features that underlie inter-specific variation and provides an indicator of their relative importance. A varimax rotation was applied to the initial solution to maximize differences in the contributions of each variable to each principal component axis (Tabachnick and Fidell, 1996). The dispersion of pteropodid and plant-visiting phyllostomid species in principal component space provides an indication of the range of morphological variation both across bats and within each group, and highlights elements of shape that are associated with that variation.

To compare each variable independently, coefficients of variation (CVs), their standard errors, and 95% confidence intervals were calculated for each group (Sokal and Rohlf, 1995). Comparing these values between groups highlights patterns of variation and conservatism within specific regions of the skull.

Results

Differentiating Pteropodids from Plant-Visiting Phyllostomids

The discriminant function analysis yielded six variables and associated coefficients that, in the presence of one another, differentiate pteropodids from plant-visiting phyllostomids. These variables are: posterior skull width, maximum zygomatic breadth, palate width at M1, dentary depth, distance from condyle to m1, and coronoid process height (Table 1). Size-adjusted values for the variables posterior skull width, palate width at M1, and coronoid process height differ significantly between pteropodids and plant-visiting phyllostomids; pteropodids have relatively narrower skulls and palates and taller coronoid processes than do phyllostomids (Table 2). The remaining three variables do not vary

TABLE 1. Results of stepwise discriminant function analysis of 19 linear, size-adjusted, cranial shape variables comparing pteropodids and phyllostomids. Abbreviations: PSW = posterior skull width, MZB = maximum zygomatic breadth, PM1 = palate width at M1, DD = dentary depth under m1, CM1 = distance from the condyle to m1, CPH = coronoid process height. Probability level: * = $P < 0.05$, ** $P < 0.01$, *** = $P < 0.001$

Predictor variable	Correlation with discriminant function	Univariate $F_{[1,46-40]}$	Pooled within-group correlations				
			MZB	PM1	MDD	CM1	CPH
PSW	0.51	92.69***	0.57***	0.43**	-0.17	-0.42**	-0.42**
MZB	-0.04	74.06***		0.72***	0.30*	-0.67***	0.14
PM1	0.33	75.54***			0.36*	-0.65***	0.29*
DD	0.07	61.98***				-0.56***	0.64***
CM1	-0.09	52.46***					-0.16
CPH	-0.30	47.17***					
Canonical R	0.94						
Eigenvalue	7.54						
% Variance	100						

significantly between the two groups in the absence of the other variables.

Inspection of pooled within-group correlations among variables (Table 1) reveals a negative association between width and length variables: skulls that are relatively wide tend to be relatively short. Species that have relatively short faces also tend to have relatively deep dentaries, which, in turn, are associated with tall coronoid processes. Not unexpectedly, there are high correlations among variables that reflect skull width as well as among those that describe skull height.

The jackknife cross validation procedure correctly classified 98% of the species into their correct families. The phyllostomid *Chiroderma villosum* was incorrectly identified as a pteropodid; all other species were classified correctly.

Variation in Cranial Shape

The three principal components extracted from the combined pteropodid/phyllostomid data set accounted for 80% of the variation among species (Table 3). Forty-nine percent of interspecific variation is explained by the first principal component (PC1), which is positively associated with relative palate width and negatively associated with the distance from the condyle to the last molar. An additional 23% of the variation among species is explained by the

TABLE 2. Means and standard errors of raw cranial shape variables that contribute significantly to discriminating between pteropodids and plant-visiting phyllostomids, along with the probability that the samples are statistically identical. Abbreviations as in Table 1

Variable	Pteropodids (n = 29)	Phyllostomids (n = 19)	Probability
PSW	0.24 ± 0.009	0.50 ± 0.008	0.000[2]
MZB	0.64 ± 0.005	0.62 ± 0.128	0.451[1]
PM1	-0.18 ± 0.009	0.11 ± 0.224	0.000[1]
DD	-1.32 ± 0.190	-1.27 ± 0.163	0.307[2]
CM1	0.47 ± 0.007	0.42 ± 0.155	0.124[1]
CPH	0.30 ± 0.171	-0.24 ± 0.145	0.000[2]

[1] — single classification analysis of variance

[2] — Mann-Whitney U-test

second principal component (PC2). This axis carries high positive loadings for several relative length variables (total skull length, anterior skull length, and total dentary length) and a high negative loading for relative face breadth (i.e., maximum zygomatic breadth). The third principal component explains only 8% of the variation among species. It is negatively associated with relative coronoid process and condyle heights and positively associated with the width of the skull in the infratemporal fossa (minimum skull width).

Pteropodids and plant-visiting phyllostomids are largely segregated along PC1; pteropodids tend to have lower PC1 scores (Fig. 2). Based on the factor loadings (Table 3) pteropodids have relatively narrow palates and long distances between the condyle and m3. Phyllostomids exhibit greater variation than pteropodids along PC1, occupying 72% of the range of PC1 scores (versus 52% of the range for pteropodid scores). In contrast to PC1, pteropodids and plant-visiting phyllostomids overlap extensively along PC2 and PC3.

TABLE 3. Partial correlations of the 19 cranial shape variables with the first three principal components (PC1, PC2, and PC3). Correlations higher that 0.75 are in bold and are interpreted. The eigenvalue, percent of variance explained, and cumulative variance for each component are provided

Variable	PC1	PC2	PC3
Maximum zygomatic breadth (MZB)	.18	-.82	.18
Total skull length (TSL)	-.04	.90	.23
Anterior skull length (ASL)	-.41	.85	.03
Posterior skull width (PSW)	.74	-.07	.55
Minimum skull width (MSW)	.19	-.21	.87
Skull height (SKH)	.68	-.08	.45
Total palate length (TPL)	-.61	.69	.05
Palate width at M3 (PM3)	.64	-.37	.30
Palate width at M1 (PM1)	.79	-.44	.12
Palate width at canine (PC)	.86	-.04	.34
Dentary depth under m1 (DD)	.58	-.21	.65
Condyle height (CH)	-.20	-.01	-.91
Coronoid process height (CPH)	-.43	-.41	-.76
Condyle–m3 length (CM3)	-.78	.44	.07
Condyle–m1 length (CM1)	-.64	.57	.04
Condyle–canine length (CC)	-.61	.73	-.11
Condyle length (CL)	-.16	.21	.11
Condyle width (CW)	-.10	-.62	-.19
Total dentary length (TDL)	-.57	.75	-.08
Eigenvalue	9.26	4.42	1.47
Variance explained (%)	49	23	8
Cumulative variance (%)	49	72	80

Plant-visiting phyllostomids present both maximum and minimum values on PC2 while pteropodids occupy less than half of the range of principal component scores. Plant-visiting phyllostomids exhibit a much greater range of variation in relative face breadth, relative skull length and relative dentary length. This variation is associated with the segregation of frugivores and nectar feeders. Phyllostomid nectar feeders have relatively long, narrow skulls, whereas phyllostomid frugivores are more similar to pteropodids in having shorter, broader skulls. Among pteropodids, frugivores and nectar feeders overlap broadly along PC2.

The opposite situation occurs along PC3. Here, principal component scores for pteropodids range widely across the axis and nectar feeders tend to have higher PC3 scores than frugivores. All phyllostomids are clustered within a relatively small range. Although PC3 accounts for only a small fraction of variation among species, the relative breadth of the skull in the infratemporal fossa (i.e., minimum skull width) and the relative heights of the condyle and coronoid processes are much more variable among pteropodids than among plant-visiting phyllostomids.

Pteropodids and plant-visiting phyllostomids exhibit non-overlapping confidence intervals for ten of the 19 variables in this study (Table 4). Of these, phyllostomids exhibit greater variability in eight variables: maximum zygomatic breadth, total skull length, anterior skull length, total palate length, condyle-m1 length, condyle-canine length, total dentary length, and palate width at the canine. Posterior skull

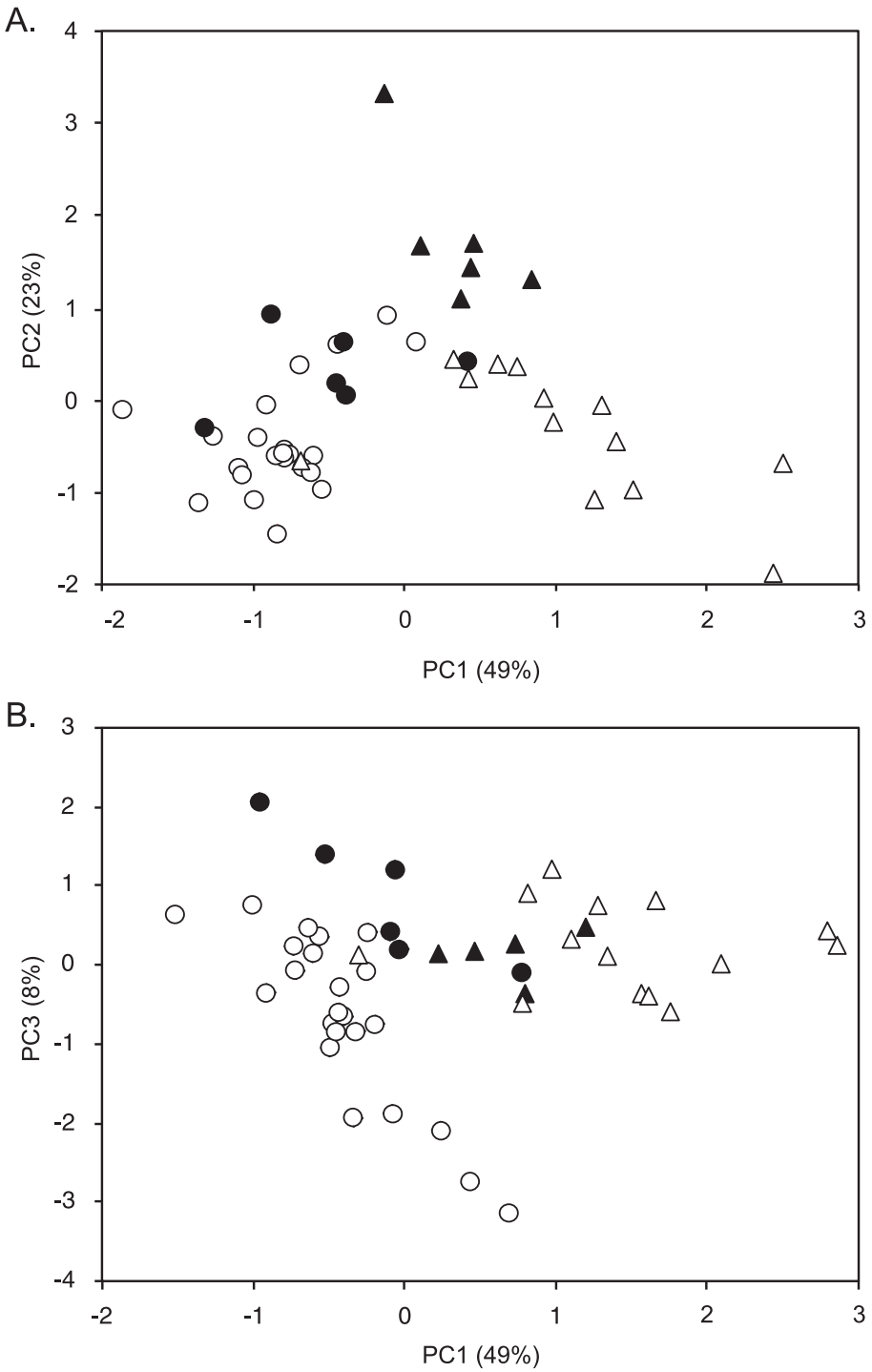

FIG. 2. The location of pteropodid (△) and plant-visiting phyllostomid species (○) in principal component space. Open symbols denote frugivores and closed symbols denote nectar feeders. A. The first and second principal components (PC1 and PC2). B. The first and third principal components (PC1 and PC3). Numbers in parentheses indicate the proportion of variation among species explained by each component

width and condyle height are more variable in pteropodids. Among the nine variables for which confidence intervals overlap, pteropodids and plant-visiting phyllostomids exhibit very similar levels of variation in minimum skull width, skull height, dentary depth, and condyle dimensions. In contrast, phyllostomids exhibit exceptionally high levels of variation in palate width (at M1 and M3) while coronoid process height is extremely variable among pteropodids. In these cases, the high level of variation in one group encompasses the confidence intervals of the other group.

Discussion

The cranial morphologies of pteropodids and plant-visiting phyllostomids represent independent evolutionary responses to selective forces favoring a plant-based diet. The differences in skull shape between the two clades reduce to general descriptors of braincase width, palate width, and the height of the coronoid process. Pteropodid skulls and palates are relatively narrow and have tall coronoid processes, while phyllostomid skulls and palates are wide and are associated with short coronoid processes. The strength of these general differences is upheld by the cross validation procedure within the discriminant function analysis. The cause of the single misclassification of *Chiroderma villosum* as a pteropodid is not clear, as this species is not an obvious outlier among phyllostomids in terms of morphology or diet.

Overall, plant-visiting phyllostomids exhibit relatively high levels of variation in many regions of the skull while cranial morphology in pteropodids is more conserved. The variation within phyllostomids reflects,

Table 4. Coefficients of variation (CV), their standard errors (SE CV), and 95% confidence intervals (L1 and L2) of size-adjusted variables for the pteropodid and plant-visiting phyllostomid species used in this study. In cases where there is no overlap in 95% confidence intervals, the highest coefficient of variation is in bold. Abbreviations for variables as in Table 3

Variables	Pteropodidae (n = 30)			Phyllostomidae (n = 18)		
	CV ± SE CV	L_1	L_2	CV ± SE CV	L_1	L_2
MZB	8.3 ± 1.10*	6.1	10.6	20.7 ± 3.52	13.6	28.0
TSL	4.8 ± 0.63	3.5	6.1	12.5 ± 2.06	8.3	16.7
ASL	6.9 ± 0.92	5.1	8.8	16.6 ± 2.76	10.9	22.2
PWS	39.8 ± 6.00	27.6	52.1	16.7 ± 2.79	11.0	22.4
MSW	74.9 ± 14.33*	45.6	104.2	63.5 ± 13.94	35.1	91.8
SKH	45.4 ± 7.09	31.0	59.9	33.0 ± 5.90*	20.9	45.0
TPL	20.0 ± 2.72	14.4	25.5	102.7 ± 29.36	42.5	162.8
PM3	59.5 ± 10.21	38.6	80.3	242.0 ± 139.93	-44.6	528.6
PM1	55.4 ± 9.23	36.5	74.2	207.4 ± 104.26	-6.1	420.9
PC	14.9 ± 2.00	10.8	19.0	51.2 ± 10.25	30.2	72.2
MDD	14.4 ± 1.92	10.4	18.3	12.9 ± 2.12	8.5	17.2
CH	34.9 ± 5.10	24.4	45.3	18.0 ± 3.01	11.8	24.2
CPH	541.6 ± 549.26	-580.0	1663.1	60.9 ± 13.03*	34.2	87.6
CM3	39.2 ± 5.89	27.2	51.2	243.3 ± 141.45	-46.4	533.0
CM1	14.7 ± 1.97	10.7	18.7	37.0 ± 6.77	23.1	15.4
CC	7.3 ± 0.97	5.4	9.3	23.6 ± 4.04	15.4	31.9
CL	12.7 ± 1.69*	9.2	16.1	19.1 ± 3.20	12.5	25.6
CW	22.0 ± 3.02*	15.8	28.2	37.9 ± 6.97	23.6	52.2
TDL	8.4 ± 1.11	6.1	10.6	24.4 ± 4.18	15.8	33.0

* — These samples failed a Shapiro-Wilks test for normality in small samples ($P < 0.05$). The 95% confidence intervals for these samples should be interpreted cautiously (Sokal and Rohlf, 1995)

at least to some extent, clear morphological distinctions between frugivores and nectar feeders. Within the morphospace defined by the first two principal components (Fig. 2), phyllostomid nectar feeders form a distinct cluster characterized by narrow faces, long skulls, and intermediate palate widths. While there is a tendency for nectar-feeding pteropodids to have lower coronoid processes and condyles than their frugivorous confamilials, the morphospaces occupied by the two trophic groups always overlap. Nectar-feeding pteropodids are more distinct from frugivorous forms in the morphospace defined by PC1 and PC3. Three nectar-feeding species exhibit exceptionally wide skulls posterior to the orbit, low condyles, and low coronoid processes. The principal components analysis supports the propositions that frugivores exhibit a broader range of cranial shapes than do nectar feeders (Dumont, 1997) and that pteropodid and phyllostomid nectar feeders are morphologically distinct (Freeman, 1995). The patterns of morphological change associated with the convergent evolution of nectar-feeding remains an interesting topic for further comparative and evolutionary analyses.

The many differences in cranial form between pteropodids and plant-visiting phyllostomids are undoubtedly influenced by a variety of historical processes. Primary among the possibilities are ecological disparities between the Old and New World tropics, the discrepancy in body size between the two clades of bats, and alternative structural constraints imposed by reliance on different sensory modalities.

Although there are broad similarities in the structure of frugivore communities in the New and Old World tropics, there are significant ecological differences between the two regions that could influence patterns of morphological diversity (Fleming *et al*., 1987). All plant-visiting bats consume non-random subsets of available plant resources and are, in that sense, specialized feeders. Nevertheless, a number of studies indicate that dietary selectivity is higher among plant-visiting phyllostomids than among pteropodids (e.g., Fleming, 1982, 1986; Willig *et al*., 1993; Utzurrum, 1995; Eby, 1998). In other words, dietary specialization is more common among phyllostomids. The fact that dietary overlap among several types of vertebrate frugivores is lower in the New World tropics led Fleming *et al*. (1987) to propose that higher spatiotemporal predictability (STP) of fruit resources may have favored the evolution of specialization in neotropical frugivores. Further evidence for the importance of STP has recently emerged in a study of community assembly rules. Fleming (2004) found that among birds and bats, there is a clear relationship between animal and plant diversity in the neotropics, whereas no such relationship exits in the Old World. From a morphological perspective, the presence of broad and highly overlapping diets among pteropodids could favor the evolution of similarity in craniofacial architecture if the diets include resources that impose similar physical demands. Alternatively, if plant-visiting phyllostomids use more exclusive subsets of available food items that exhibit unique physical properties, one can envision selection for morphological specialization and thus, diversity.

Fruit size and fruit hardness are significantly correlated (Aguirre *et al*., 2003) and are the physical characteristics most likely to be associated with variation in the morphology of the feeding apparatus. Either factor could prevent a bat from being able to consume a fruit, but hardness is most likely to be restrictive. While small bats can (and do) feed on large fruits in situ, bite force is significantly correlated with body size (Aguirre *et al*., 2002) and small bats may be unable to access relatively hard fruits.

Unfortunately, we know relatively little about the physical properties of fruits that are eaten by bats. Existing surveys of bat fruits from the New and Old World indicate that there is a great deal of overlap in hardness values, but that the hardest fruits are found in the Old World tropics (Aguirre *et al*., 2003; Dumont, 2003). This accords well with the fact that Old World fruits are larger than New World fruits (Fleming *et al*., 1987; Mack, 1993). In this respect, it is notable that vertebrate frugivores in the Old World are larger than their New World counterparts (Fleming *et al*., 1987). Bats are no exception to this rule and it is not unreasonable to suggest that body size has played a significant role in the evolution of morphological diversity among plant-visiting bats.

As noted above, one consequence of increased body size is increased bite force. Large bats can produce absolutely larger bite forces and, therefore, have the potential to access a much broader range of fruit resources than can small bats. Given the limitations imposed by small size, small-bodied species may encounter selective pressure for morphological and/or behavioral specialization in order to optimize bite forces and increase the efficiency of food processing. Specialized feeding behaviors have been documented for several small-bodied species that specialize on hard fruits (Dumont, 1999; Dumont and O'Neal, 2004). Similar pressures may be lacking in large-bodied forms, which overcome mechanical obstacles simply by virtue of their strength. In the case of plant-visiting phyllostomids, the combination of small size and increased dietary specialization could simultaneously promote the evolution of morphological diversity. On the other hand, pteropodids, with their generally larger size and broader diets, may not have encountered similar selective pressures. It is important to point out that not all pteropodids are large and there are many species that weigh less than 100 grams. That these small-bodied species tend to exhibit more specialized cranial morphologies than do larger-bodied forms provides circumstantial support for the idea that body size plays a role in morphological specialization and diversity in plant-visiting bat assemblages.

In addition to body size, it is possible that the relatively taller condyles and coronoid processes of pteropodids allow them to produce relatively higher bite forces than can phyllostomids. Increased head height is associated with increased bite force production in xenosaurid lizards (Herrel *et al*., 2001). Similar associations have not been investigated in mammals, but it is reasonable to hypothesize that taller condyles and coronoid processes create space for the attachment of larger jaw adductors and, thus, potentially increase bite forces. Circumstantial support for this hypothesis is found in reduced major regression analyses of size adjusted coronoid process height against head volume [(total skull length $\times$ maximum zygomatic breadth $\times$ skull height)$^{1/3}$]. Within each family, nectarivores consistently exhibit lower than expected values of relative coronoid process height than frugivores of similar size. This accords well with the fact that nectarivores produce relatively low bite forces per unit of body mass (data from Aguirre *et al*., 2002 and Dumont and Herrel, 2003).

Yet another potential influence on different levels of diversity in craniofacial form within the two clades of plant-visiting bats is their reliance on different sensory modalities. The skull is not simply a tool for feeding, but accommodates the competing demands of the visual, olfactory, and auditory systems as well as the brain (e.g., Hoyte, 1987; Neuweiler, 2000; Pedersen, 2003; Reep and Bhatnagar, 2003). As outlined in the introduction, all plant-visiting

bats studied thus far use smell to locate plant resources (e.g., Rieger and Jakob, 1988; Laska, 1990; Acharya *et al*., 1998; Luft *et al*., 2003). Pteropodids also have relatively large eyes and rely heavily on vision during foraging (Neuweiler, 2000). Among primates, which are also highly visual, the presence of low strains in the circumorbital region of the skull during feeding has led to the suggestion that well-defined bony orbits serve to protect the eyes rather than to transfer forces generated during feeding (Hylander *et al*., 1991; Ravosa *et al*., 2000; Ross, 2001). Although pteropodids do not exhibit the same degree of orbital convergence and frontation that is seen in primates and some carnivores (Noble *et al*., 2000), the need to support and protect their large eyes may limit potential re-arrangements of the skull. If supporting a large eye does impose a structural constraint, then the de-emphasis on vision in favor of specializations for echolocation among phyllostomids may have opened the door to the evolution of diversity in craniofacial form. Although significant differences in cranial morphology are associated with the oral and nasal emission of echolocation sounds (Pedersen, 1993, 1998), the lack of correlation between facial features and echolocation call parameters suggest that echolocation may not impose strong boundaries on facial shape (Goudy-Trainor and Freeman, 2002).The contrasting emphasis on vision and echolocation in pteropodids and plant-visiting phyllostomids provides an opportunity to evaluate the impact of these systems on cranial morphology; comparative analyses of routine strain in the facial skeletons of bats are underway.

This study describes patterns of morphological diversity in the skulls of pteropodids and plant-visiting phyllostomids. Much more work is needed before we will understand the historical processes that underlie these patterns. Additional data summarizing the structure of New and Old world plant communities, dietary breadth, the physical properties of plant resources, body size, bite force, and comparative craniofacial biomechanics are urgently needed. It is critical that any inquiry into the evolutionary processes underlying patterns of diversity be based firmly in a well-defined phylogenetic context. In this light, it is interesting that recent developments in chiropteran systematics suggest novel interpretations of pteropodid relationships that require reinterpretations of the evolution of phytophagy in bats.

Pteropodids have long been identified as the most primitive clade of extant bats and are considered to be an ancient lineage (see review in Simmons and Geisler, 1998). In this context, their morphological conservatism suggests that they are, in some sense, 'primitive' bats that have not been released by the key innovation of echolocation. More recently, new molecular evidence suggests that pteropodids are closely related to rhinolophoid bats and, like phyllostomids, are derived from echolocating ancestors (Hutcheon *et al*., 1998; Teeling *et al*., 2000, 2002; Van Den Bussche *et al*., 2002). If this is the case, then pteropodids may represent a much more recent radiation than was previously believed. Freeman (2000) suggested that the evolution of phytophagy among phyllostomids constituted an escape from the constraints of insectivory and promoted morphological diversification. If pteropodids represent a similar radiation in the paleotropics, then the question of why they are so much less diverse becomes even more intriguing. Finding an answer to this question will require analyses of many different data sets within a phylogenetic context that includes not only well-supported topologies but accurate assessments of branch lengths and divergence times for both lineages of plant-visiting bats.

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Appendix

Morphometric data were collected from specimens housed at the American Museum of Natural History (AMNH), the National Museum of Natural History (NMNH), and Carnegie Museum of Natural History (CM), the Papua New Guinea National Museum and Art Gallery (PNGMR), the University of Papua New Guinea (UPNG), and the Australian Museum (AM). Specimens with the designation 'ERD' were collected by the author and will be accessioned into the collections of the Carnegie Museum of Natural History. The sex of specimens is indicated in parentheses following the specimen number. Taxonomy follows Wetterer *et al*. (2000) for phyllostomids and Koopman (1993) for pteropodids

Family Phyllostomidae: *Ametrida centurio*, AMNH 187224(♂),187225(♀); *Anoura geoffroyi*, CM 99159(♀), 99160(♂), 99162(♂), 99165(♀), 99166(♀), 99178(♀), 99182(f), 99187(♂), 99193(♂), 99195(♂); *Ardops nichollsi*, AMNH 213925(♂), 213954(♂); *Ariteus flaviscens*, USNM 545168(♂), 545169(♂), 545172(♀), 545173(♂), 545175(♂), 545176(♀); *Artibeus jamaicensis*, ERD 135(♀), 136(♀), 149(♂), 150(♂), 151(♂), CM 99705(♂), 99706(♀), 99707(♀), 99708(♂), 99709(♂), 99710(♀), 99711(♀), 99718(♂), 99719(♂), 99720(♂), 99724(♀); *Brachyphylla cavernarum*, AMNH 188234(♂), 188235(♂), 213983(♀), 214014(♀), USNM 544828(♀), 544829(♂), 544830(♂), 544831(♀), 544832(♀), 544833(♂); *Carollia perspicillata*, ERD 139(♂) 140(♂), 145(♂), 147(♀), 152(♂), CM 99465(♂), 99466(♂), 99467(♂), 99468(♂), 99469(♀), 99470(♀), 99471(♀), 99472(♀), 99473(♂), 99474(♀); *Centurio senex*, CM 55231(♂), 55730(♂), 55732(♀), 90535(♂), USNM 508827(♀), 511473(♂), 511475(♀), 511476(♀), 565040(♂), 565041(♀); *Chiroderma villosum*, AMNH 209561(♂), 209562(♂), 209563(♂), 209564(♀), 209566(♀), 209569(♀), 214417(♂), 235313(♀), 235314(♀), 235315(♂); *Choeroncteris mexicana*, CM 80212(♂), 93662(♀); *Erophylla sezekorni*, AMNH 23763(♂), 41062(♂), 41065(♂), 41095(♀), 41096(♀), 45191(♀); *Erophylla sezekorni*, USNM 300516(♀), 300518(♂); *Glossophaga soricina*, ERD 146(♀), CM 99224(♀), 99229(♀), 99230(♂), 99231(♂), 99233(♂), 99234(♂), 99235(♂), 99239(♀), 99246(♀), 99248(♀); *Leptonycteris nivalis*, CM 17672(♂), 80216(♂), 80219(♀), 80221(♀); *Mesophylla macconnelli*, AMN48269(♂), 48270(♀), 76565(♀), 76569(♂), 208073(♀), 246626(♀), 248886(♂), 248887(♂), 262540(♀), 262541(♂); *Phyllonycteris poeyi*, AMNH 23758(♂), USNM 103581(♂), 103583(♀), 300514(♀); *Platyrrhinus helleri*, CM 79428(♂), 79429(♀), 90561(♀), 90562(♀), 90563(♀), AMNH 230635(♂), 268542(♂); *Pygoderma bilabiatum*, USNM 105685(♀), 115067(♂), 234290(♀), 234291(♂), 234294(♂), 234295(♀), 234297(♂), 460507(♀), 552731(♀); *Rhinophylla pumilio*, AMNH 266171(♀), 266187(♂),USNM 574529(♂), 574530(♂), 574531(♀), 574532(♀), 574533(♂), 574535(♀); *Sturnira lilium*, CM 42831(♀), 42833(♀), 42834(♂), 42839(♀), 42842(♂), 42850(♂), 42861(♀), 42862(♀), 42873(♂), 72334(♂), 72346(♂), 72349(♂), 72351(♀), 72352(♀), 72353(♀).

Family Pteropodidae: *Acerodon jubatus*, USNM 125297(♀), 125298(♂); *Aethalops alecto*, AMNH 216757(♀), 216758(♀), 216765(♀), USNM 481331(♂), 481332(♀); *Chironax melanocephalus*, USNM 481035(♀), 481037(♀), 481038(♀), 481347(♀), 481348(♂), 481349(♀); *Cynopterus brachyotis*, AMNH 103211(♂), 103212(♀), 103213(♀), 103214(♀), 103216(♂), 103218(♂), 103219(♀), 103220(♂), 103222(♂); *Dobsonia minor*, ERD 137(♀), 138(♀), 144(♂), PNGMR 23796(♂), 23801(♀), AMNH 105172(♂), 105174(♂), 105175(♂), 152440(♀), 152443(♀); *Eidolon helvum*, CM 40990(♀), 86648(♂), 86649(♀), 102020(♂), 102021(♀), 102022(♀), AMNH 119157(♂); *Eonycteris spelaea*, AMNH 216770(♀), 216772(♂), 233977(♀), 233980(♀), 238193(♂), 238195(♂); *Epomophorus minor*, CM 40959(♀), 40961(♀), 40962(♂), 57665(♀), 57666(♂), 102024(♂), 102025(♀), 102042(♂), 102043(♂); *Epomops franqueti*, CM 62374(♂), 107991(♀); *Haplonycteris fischeri*, USNM 356627(♀), 458170(♀), 458171(♀), 458172(♂), 458173(♀), 458178(♂); *Harpyionycteris whiteheadi*, USNM458214(♀), 458216(♂); *Megaerops niphanae*, AMNH 87285(♀), 87290(♂), 87291(♀), 238183(♂); *Megaglossus woermani*, CM 90780(♀), 90783(♂); *Melonycteris melanops*, AMNH 194325(♂), USNM 580029(♂), 580030(♀); *Micropteris pusillis*, CM 40984(m), 40986(♂), 40987(♂), 58242(♂), 58251(♀), 69147(♂), 90759(♀), 90761(♀), 90763(♀), 90773(♀); *Myonycteris torquata*, AMNH 236236(♂), 236239(♀), 236240(♀), 236242(♂), 236243(♂), 236244(♀); *Nanonycteris veldkampi*, USNM 411792(♂), 411795(♀); *Notopteris macdonaldi*, FMN31577(♂), USNM 260072(♀), 260079(♀);

APPENDIX. Continued

Nyctimene albiventer, UPNG 407(♀), 2918(♀), 3112(♂), PNGMR 22115(♂), 22493(♂), 23602(♀), 23603(♂), AMNH 105097(♀), USNM 543256(♂), 543260(♀); *Otopteropus cartilagonodus*, USNM 573439(♂), 573440(♀), 573441(♀), 573442(♀), 573444(♂), 573445(♂); *Paranyctimene raptor*, PNGMR 23797(♀), 23808(♂), AMNH 160315(♀), 191300(♂), 191301(♂), 191302(♂), 191303(♀), 194855(♀), 194856(♀), 198634(♂); *Pteralopex anceps*, AM 6282(♂), 6283(♂), 6347(♀), 6498(♀); *Pteropus conspicillatus*, AMNH 108864(♀), 154540(♀), 154541(♂), 154542(♂), 154544(♀), CM 111913(♀), 111914(♀), 111917(♂), 111919(♂), 111920(♂); *Rousettus aegyptiacus,* CM 46693(♂), 46694(♂), 78789(♂), 78792(♂), 78800(♀), 78801(♂), 78802(♀), 78805(♀), 102101(♂), 102102(♀); *Scotonycteris zenkeri*, AMNH 239379(♂), 239380(♀), 239381(♀), 239382(♂), 256535(♀); *Sphaerias blanfordi*, USNM 564428(♀), 564429(♀), 564431(♂), 564432(♀), 564433(♂), 564439(♂); *Styloctenium wallacei*, AMNH 153126(♀), 153129(♀), 153130(♀), 222978(♂), 222979(♂); *Syconycteris australis*, PNGMR 23834(♂), 24582(♂), 24583(♂), 24605(♂), 24611(♀), 24617(♀), AMNH 194309(♀), 194320(♀), 194323(♂), 198628(♀); *Thoopterus nigrescens*, USNM 199794(♀), 199795(♀), 199798(♂), 199799(♂), 217079(♂), 217441(♀).