Wings of fringed fruit-eating bats (*Artibeus fimbriatus*) are highly integrated biological airfoils from perspectives of secondary-sexual dimorphism, allometry and modularity

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Phenotypic variability is ubiquitous. This is especially true in bats where families such as Phyllostomidae encompass as much phenotypic variability as some entire orders of mammals. Typically, phenotypic variability is characterized based on cranial morphology with studies of other functionally important aspects of the phenotype such as legs, feet and wings less frequent. We examined patterns of secondary-sexual dimorphism and allometry of wing elements of the fringed fruit-eating bat (*Artibeus fimbriatus*) as well as examined for the first time modularity of bat wings. Patterns were based on 13 wing measurements taken from 21 female and 15 males from eastern Paraguay. From a multivariate perspective *A. fimbriatus* exhibited significant secondary-sexual dimorphism. Females were larger than males for all 13 wing characteristics with significant differences involving the last phalanx of the 4^{th} and 5^{th} digits. Female wings were also relatively larger than male wings from a multivariate perspective as well as the last phalanx of the 4^{th} and 5^{th} digit, after adjusting for wing size based on forearm length. Wing elements were highly variable regarding allometric relationships with some exhibiting no allometric patterns, and others exhibiting isometry or hyperallometry depending on the element. Wings exhibited significant modularity with metacarpals, proximal phalanges and distal phalanges each representing a discrete module. Wings of *A. fimbriatus* exhibit substantive patterns of dimorphism, allometry and modularity. While the Big Mother Hypothesis is a strong theoretical construct to explain wing dimorphism, there is yet no sound theoretical basis to patterns of allometry and modularity of the wing. Indeed, trying to understand the determinants of variation in wing morphology is ripe for future investigation.

INTRODUCTION

Phenotypic variation is ubiquitous across the historical and contemporary biota (Alroy, 1998; Foote, 1997; Endler, 1978). While such variation results from underlying genetic differences, differential expression and ultimately developmental heterochrony among organisms, it manifests in many forms such as interspecific discontinuities (Sokal and Sneath, 1963), sexual dimorphism (Ralls, 1976), and clinal variation along gradients (Endler, 1978), to name only a few. In mammals, the skull (i.e., cranium and mandible) is often the focus of morphometric analysis for many reasons. First, in many situations the skull or parts therein have evolved and diversified more rapidly than other phenotypic structures (Cheverud, 1982; Hallgrimsson et al., 2007; Linde-Medina et al., 2016). This stems from the fact that characteristics of the skull determine in many cases performance of the organism, in particular in obtaining and processing food (Freeman, 1988; Dumont et al., 2012; Santana et al., 2010), one of the most basic of biological processes. Rapid adaptive evolution can lead to conspicuous discontinuities among even closely related species and for this reason skull features are often the first go-to when distinguishing taxa, constructing dichotomous keys for identification, and ultimately classifying them into larger taxonomic groups.

Bats offer an ideal example of this phenomenon. Bats have evolutionarily radiated to assume perhaps the greatest amount of phenotypic variability of any order of Mammalia (Dumont et al., 2011). Contributing to this is the single family Phyllostomidae that exhibits the greatest variability, phenotypic as well as reproductive, ecological, and geographic, of any family level clade in the class (Baker et al., 2003). Skull-related phenotypic variability can be described as an impressive adaptive radiation that has conferred high species richness on phyllostomid bats and allowed them to enter new adaptive zones characterized by carnivory, frugivory, insectivory, nectarivory, and sangunivory (Dumont et al., 2012). Indeed, the scientific literature is replete with examples of how the relationship between form and function in skulls of phyllostomid bats is related to performance (Freeman, 1988; Aguirre et al., 2003; Santana et al., 2010) that is true across many scales of biological organization from the entire clade (Dumont et al., 2005; Nogueira et al., 2009) to individual local communities (Aguirre et al., 2002). Despite this focus on the skull, other trophic apparatuses characterize the phyllostomid phenotype, some of which are equally as important as the skull but less appreciated and certainly less studied.

Wings form an important performance-related apparatus in bats (Norberg and Rayner, 1987). For example, wing loading (mass/area of the wing) and aspect ratio (wingspan^2/area of the wing) define important differences in wing morphology related to efficiency of flight, speed, and maneuverability (Norberg, 1981). Accordingly, bats can be assigned to different feeding guilds based on wing morphology that reflect effects of performance on trophic ecology (Findley et al., 1972; Norberg and Rayner, 1987; Kalko et al., 1996; Castillo-Figueroa, 2020). Fewer efforts have been made for wings than skulls to try to understand determinants of phenotypic variability. Nonetheless, it has been demonstrated that wing morphology is highly integrated from a number of perspectives. For example, embryonic development of bat wings is concerted with different elements such as metacarpals, proximal phalanges and distal phalanges ossifying at different times and rates (Adams, 2000). Many species of bats exhibit sexual dimorphism in wing morphology putatively related to performance when carrying a large fetus or neonate (Ralls, 1976; Camargo and Oliveira, 2012). This idea is further supported by allometric relationships of litter mass that are influenced by flight performance of females in microbats (Hayssen and Kunz, 1996). In some species wing elements are even relatively larger in females than males after controlling for body size (Stevens et al., 2013), further suggesting a performance component to dimorphism. Within species, wing morphology is geographically variable and related to environmental gradients (Stevens et al., 2016; Conenna et al. 2021).

Herein, we examine sexual dimorphism, allometry and modularity of wings of the fringed fruit-eating bat (*Artibeus fimbriatus*) from eastern Paraguay. While sexual dimorphism in wing morphology has been examined for a number of bats species, even within the genus *Artibeus*, nothing is known for *A. fimbriatus*. Much less is known of allometry and modularity of bat wings. Differences in wing morphology, especially those related to differences in basic aerodynamic characteristics such as aspect ratio, are the results of differences in the relative lengths of the metacarpals and phalanges (Castillo-Figueroa, 2020) that likely could not result from isometry. Thus, better understanding allometric relationships among wing bones will better illuminate how variation in aerodynamic characteristics result. Similarly, nothing is known about the modularity of bats wings. A module is a group of traits that are more integrated (i.e., exhibit more covariation) among themselves than they are to other traits outside the group (Eble, 2005; Esteve-Altava, 2017). Different elements are involved in different aspects of flight. For example, concerted actions of the metacarpals are important for lift whereas concerted action of the distal phalanges is important for maneuverability (Camargo and Oliveira, 2012). Also, these different kinds of wing elements ontogenetically develop in concert but with different timing (Jones, 1967; Adams 1992), further suggesting modularity. We make three predictions regarding variation in wing morphology of *A. fimbriatus*. First, females should exhibit greater absolute and relative sizes of wing elements that are consistent with the added burden of carrying a large fetus/neonate. Second, bat wings should be integrated via allometry, but isometry will not necessarily define associations. Third, bat wings will exhibit modularity with respect to three groups of wing elements (metacarpals, proximal phalanges, distal phalanges) whereby within module correlations will be significantly greater than among module correlations.

While not the largest, *A. fimbriatus* is a large species for the genus with a distribution that is limited to Atlantic Forest of South America and a few scattered records in the bordering Chaco of Argentina. While common, there is little information in the literature on the biology of this species. It often exhibits intermediate abundance across its distribution based on mist netting records (Muylaert et al., 2017). The species can be classified as a highly cluttered space gleaning frugivore based on the scheme of Kalko et al. (1996) and likely is disproportionately an upper canopy forager (Gregorin et al., 2017). The frugivorous diet of *A. fimbriatus* is composed primarily of fruits of the genera *Ficus* and *Cecropia* (Bello et al., 2017; Stevens and Amarilla-Stevens, 2021). Based on few data (Esberard et al., 1998; Lima and Fabien, 2016) this species likely exhibits a seasonally polyestrous reproductive cycle. Based on direct observation (Trajano, 1996; Arnone, 2008; Esberard et al., 2014) and circumstantial evidence such as ectoparasite loads (Weber et al., 2011), *A. fimbriatus* tends to roost in caves and tree holes (Garbino and Tavares, 2018). Herein, we expand the body of information on *A. fimbriatus* by describing phenotypic variability associated with the wing and use this species as an example of how more generally wings of bats are highly integrated trophic structures.

MATERIALS AND METHODS

Bats were collected from the Reserva Natural Del Bosque Mbaracayú (24°07.69'S, 55°30.34'W) and Yaguarete Forests (23°48.50'S, 56°07.68'W) in the departments of Canindeyú and San Pedro, respectively, in eastern Paraguay from 1996 to 1998. Bats were handled and euthanized following guidelines of the American Society of Mammalogists (Sikes et al., 2016). Voucher specimens were deposited in the Natural Science Research Laboratory of the Museum of Texas Tech and in the Museo Nacional de Historia Natural del Paraguay.

We examined 21 female and 15 male *A. fimbriatus*. For each individual we measured length of forearm (FA); length of the first digit (P1); length of the metacarpal of the second digit (P2); length of the metacarpal (P3.1), first (P3.2), second (P3.3) and third (P3.4) phalanx of the third digit; length of the metacarpal (P4.1), first (P4.2) and second (P4.3) phalanx of the fourth digit; and length of the metacarpal (P5.1), first (P5.2) and second (P5.3) phalanx of the fifth digit. Measurements were made two non-consecutive times for each specimen and values across the two replicates were averaged for use in subsequent analyses. All variables were transformed to the log base 10.

We examined both absolute and relative secondary sexual dimorphism in wing morphology. We used multivariate analysis of variance (MANOVA) to determine significant differences between multivariate centroids between males and females. This was followed by individual analyses of variance (ANOVA) for each character (P1-P5.3) to infer those that likely contributed to the multivariate difference. We used multivariate analysis of covariance (MANCOVA) followed by individual analyses of covariance (ANCOVA) to examine relative differences between females and males after accounting for differences in overall size. Overall size was estimated based on forearm length. We tested for homogeneity of variances and covariance matrices based on Levene's tests (Levene, 1960) and the Box's M test (Box, 1949), respectively. Tests of secondary sexual dimorphism and underlying assumptions were conducted in SPSS version 24 (IBM Corp., 2016).

We used major axis regression (Pearson, 1901) to estimate allometric variation in wing characteristics. Major axis regression is more appropriate than ordinary least squares regression in this case because both independent and dependent variables are measured with error. Major axis regression models residual variation on both the y- and x-axis, not just the y-axis as with ordinary least squares (Warton et al., 2012). In these regressions, forearm length was the independent variable and each of the remaining wing characteristics were dependent variables in individual analyses. We used the R package "smart" (Warton et al., 2012) to conduct the major axis regression as well as to test for differences from isometry (i.e., Ho: $b_1 = 1$).

We used the covariance ratio (CR, Adams, 2016) and permutation test to examine modularity of elements of bat wings. We assumed that wings were comprised of three different modules: 1) metacarpals (P2.1, P3.1, P4.1, P5.1), 2) first phalanges (P3.2. P4.2. P5.2), and a third module comprised of the distal phalanges of digits 3-5 and the second phalanx of digit 3 (P3.3, P3.4, P4.3, P5.3). The covariance ratio measures the relative contributions of within and among module integration whereby modularity is defined by significantly more within module covariance than among module covariance. The expected covariance ratio under the null hypothesis of no modularity is approximately one and deviations from unity characterize significant modularity. Significance of the covariance ratio was determined based on permutation. Accordingly, membership of wing elements to modules was permuted and the covariance ratio recalculated. This was repeated 10,000 times to generate a distribution of randomly permuted covariance ratios and the actual covariance ratio was compared to this distribution to generate a probability of the observed covariance ration given the null hypothesis. Covariance Ratios and their significance were determined in the R package "geomorph" (Adams et al. 2022).

RESULTS

Individual *A. fimbriatus* were variable in terms of wing morphology (Table 1). A significant multivariate absolute difference existed between sexes ($F_{13,22} = 2.53$, $P = 0.026$). Significant univariate differences between males and females in the length of the distal phalanx of digits 4 and 5 indicated that these wing characteristics most likely contributed to the multivariate difference between sexes. MANCOVA indicated that adjusting for differences in forearm length significantly accounted for at least a portion of the absolute difference between among individuals ($F_{12,22} = 3.36$, $P = 0.0070$. Significant relative differences between sexes remained after individual differences regarding forearm length were accounted for ($F_{12,22}$, $P = 0.022$). ANCOVA indicated that relative differences in distal phalanx of digits 4 and 5 likely contributed to the multivariate difference.

Significant allometric relationships with forearm length existed for seven of twelve wing characteristics (Table 2). Those elements not exhibiting allometric relationships were the first digit, the second phalanx of digit 3 and the most distal phalanges of the third, fourth, and fifth digits. Slopes of allometric relationships for the metacarpals of digits three, four, and five did not significantly differ from one, thus exhibiting isometry. Allometric relationships involving the metacarpal of the second digit and the first phalanx of digits three, four, and five were characterized by slopes that were significantly greater than one, thereby exhibiting hypeallometry. Similar patterns of allometry for three subsets of wing elements, namely the third metacarpal (P3.3) and phalanges (P3.4, P4.3, P5.3), metacarpals (P2, P3.1, P4.1, P5.1), and second metacarpals (P3.2, P4.2, P5.2) suggest that these groups of elements may represent modules.

The overall modularity test of the three different modules indicated significant modularity of the wing (CR= 0.52, $p < 0.001$). Three pairwise contrasts were also significant

(P3.3 and distal phalanges versus metacarpals, CR=0.35, P = 0.016; first phalanges versus P3.3 and distal phalanges, CR=0.52, P = 0.014; metacarpals versus first phalanges, CR=0.68, P = 0.014) suggesting that all three modules contributed to significance of the overall test.

DISCUSSION

Elements of the wing of *A. fimbriatus* exhibit considerable variation and despite the mosdes sample sizes obtained for this analysis we could demonstrate that such variation was significantly related to secondary-sexual dimorphism, allometry, and modularity. Such integrated and structured variation suggests that the wing of bats is a finely tuned airfoil whose morphology reflects variation in size but also flight performance.

Patterns of secondary-sexual dimorphism

Significant sexual dimorphism in the wing of bats whereby elements of females are larger than males is common (Myers, 1978; Williams and Findley, 1979; Willig, 1983; Castillo-Figueroa, 2018) and likely reflects evolutionary responses to the added burden of carrying a large fetus and subsequently a large neonate (Ralls, 1976). Only distal elements were significantly different between males and females in *A. fimbriatus* based on univariate tests. Nonetheless, these differences involving the distal portion of both the fourth and fifth digit were consistent. Larger wingtips allow for greater propulsion (Findley et al., 1972) and agility (Altringham, 1996) that may be needed by mothers during development of offspring.

With the exception of the thumb, the same wing elements for *A. lituratus* were examined by Stevens et al. (2013) as for *A fimbriatus* examined here. Overall, *A. lituratus* exhibited sexual dimorphism whereby females are larger than males, a pattern that is common for bats (Ralls, 1976). As with *A. fimbriatus*, *A. lituratus* exhibited both absolute and relative (after controlling for body size) size dimorphism for the last elements of digits four and five. Despite these similarities these two species were also somewhat different in their expression of dimorphism. *Artibeus lituratus* also exhibited significant absolute and relative dimorphism for the metacarpals of digits 3, 4, and 5 as well as the most distal phalanx of digit 3. *Artibeus lituratus* also exhibited an absolute difference in metacarpals of digit 2 and 3. Thus, both species exhibit significant sexual dimorphism, but may do so in different ways and based on different wing elements. It is important to note that error degrees of freedom were more than an order of magnitude greater for the study on *A. lituratus* than for this study on *A. fimbriatus*, so examinations of only patterns of significance may be suspect.

Patterns of allometry

Bats in general exhibit strong patterns of allometry with respect to a number of different structures of ecological or evolutionary significance (Norberg, 1981; Silva, 1998; Hendrick and Dumont, 2018). For example, cranial morphology of nectarivorous bats of Phyllostomidae exhibit varying patterns of hypo-, iso-, and hyper-allometry that varies by subfamily and appears to have a strong phylogenetic component (Bolzan et al., 2015). Echolocation calls are often negatively allometrically related to body size in a number of families (Novick, 1977; Lopez-Cuamatzi et al., 2020), likely due to larger bats needing more space to maneuver and lower frequency echolocation calls allowing detection at farther distances (Heller and von Helverson, 1989; Barclay and Brigham, 1991; Thiagavel et al., 2017). There is an allometric component to variation in male genitalia, especially for species where copulation occurs while females are hibernating (Lupold et al., 2004). Litter mass in microchiropterans scales with aerodynamic characteristics of wing area and wing loading (Hayssen and Kunz, 1996), that themselves scale with size (Norberg and Rayner, 1987). Nonetheless, as pointed out by Castillo-Figueroa (2020), such aerodynamic characteristics are the result of variation in the actual wing elements and more direct examination of patterns of allometry of these elements may provide richer insights.

Patterns of allometry of many but not all wing elements were substantive and significant. In particular, metacarpals (P3.1, P4.1, P5.1) exhibited isometry whereas first (P3.2, P4.2, P5.2) and metacarpal of digit 2 exhibited hyperallometry, whereby size of the element increased at a faster rate than overall size based on forearm length. Distal elements (P3.3, P3.4, P4.3, P5.3) did not exhibit allometric relationships (i.e., slopes and r^2 no greater in magnitude than expected by chance). That the same elements across digits (i.e., P3.1, P4.1, P5.1) exhibited the same pattern of allometry that is different than other elements (i.e., P2, P3.2, P4.2, P5.2) suggests similar influences of selection on performance related characteristics or similar patterns of development and ossification (Adams, 2000). Bat wings exhibit compensatory growth during development (Adams, 1992). Moreover, distal wing bones such as the phalanges undergo chondrogenesis and ossify later in development than more proximal wing bones (Adams, 1992, 2000). As a result, more distal elements bear most of the burden of compensation and are thus the most variable (Adams, 1992). Compensatory growth also manifests as differences in the form of allometric relationships between different groups of wing elements and likely explain the lack of relationships of distal elements with overall size.

PATTERNS OF MODULARITY

Phenotypic modularity is a common phenomenon across Mammalia (Goswami, 2006; Porto, 2009; Koyuba et al., 2014) and often identifies performance-related integrated structures that are under selection (Melo and Marroig, 2015). Indeed, much focus has been on cranial and mandibular morphology in mammals in general, but also in bats in particular (Lopez-Aguirre et al., 2015). The cranium is often composed of at least two modules, the neurocranium and the splachnocranium that are related to patterns of muscle insertion and brain development on the neurocranium and radiation in dentition and morphology of the rostrum that is related to foraging ecology on the splachnocranium (Lopez-Aguirre et al., 2015). Similarly, the mandible is often comprised of two modules, the ascending ramus and the alveolar region that are related to differences in performance-related specialization for biting and food manipulation, respectively (Lopez-Aguirre et al., 2015). Modularity of the cranium and mandible illuminate how evolutionary and developmental trends translate into performance-related patterns describing the relationship between form and function.

Similarly, the wing exhibits strong patterns of modularity, at least for *A. fimbriatus*, that may be general across bats. Moreover, at least three modules make up the wing of *A. fimbriatus* based on these analyses. Different sets of wing elements (i.e., metacarpals, proximal, and distal phalanges) are related to different aspects of the performance of the wing while in flight. For example, wing tips represented by P5.3, P4.3, P3.4, and probably P3.3, are the primary propulsive portion of the chiropteran wing whereby longer wingtips are related to greater speed (Findley et al., 1972; Altringham, 1996). In contrast, metacarpals are important for generation of lift (Findley et al., 1972) and the relative length of metacarpals defines the degree to which curvature of the wing is located toward the trailing edge of the wing, which influences maneuverability (Stockwell, 2001). To this end, it is intuitive that different groups of wing elements are important for different aspects of flight and thus exhibit modularity. This is the first demonstration of modularity of bat wings of any species. Indeed, modularity may be the product of natural selection fine-tuning particular sets of structures so as to enhance performance during flight. Nonetheless, sets of elements develop and ossify at different rates (Adams, 1992). Future study should examine generality of modularity as well as try to tease apart ecological, evolutionary, and developmental determinants to better understand the mechanistic bases to these patterns.

Bat wings are highly variable trophic and performance-related phenotypic structures. From a morphometric perspective, much less variation in wing morphology has been characterized relative to other structures such as the cranium, mandible, or teeth and as a result determinants of wing morphology are much less understood from theoretical perspectives based on development and evolution. For example, while a number of studies have characterized sexual dimorphism of bat wings, many fewer have examined allometry, and this study is the first to examine modularity. There is somewhat of a theoretical basis to begin to explain patterns of sexual dimorphism, but only much more incomplete theoretical constructs can inform the mechanistic basis of patterns of wing allometry and modularity. Given the substantive variability of bat wings and the variety of different influences that range from ecological, evolutionary, and developmental, this aspect of the chiropteran phenotype is ripe for further morphometric investigation.

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DATA AVAILABILITY

The data are available from the corresponding author on reasonable request.

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Figure Legend

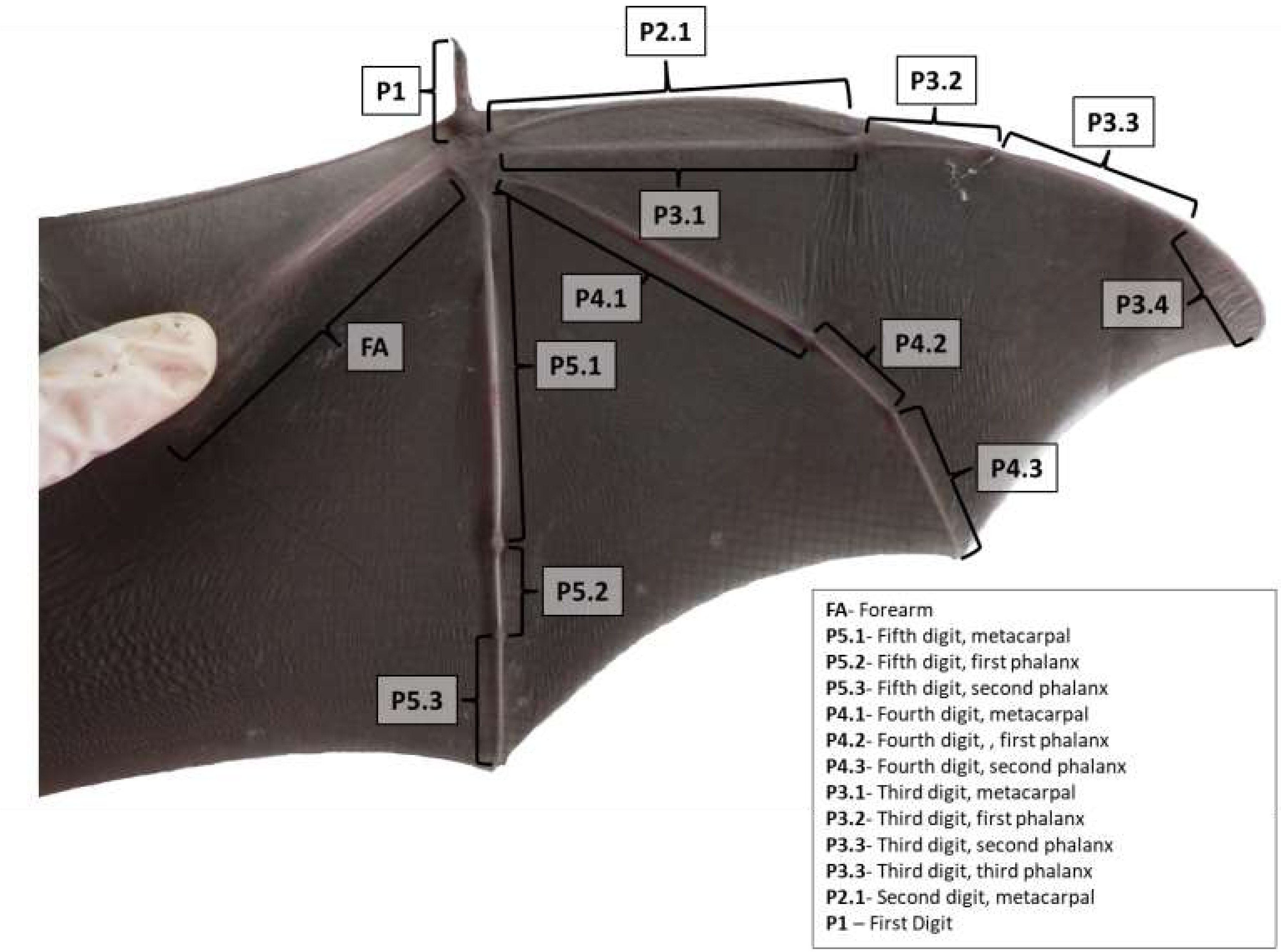
Figure 1. Elements examined when characterizing sexual dimorphism, allometric relationships and modularity of wings of *Artibeus fimbriatus*.

Table 1.—Results from multivariate analysis of variance (MANOVA) and univariate analysis of variance examining differences in absolute (MANOVA) and relative (MANCOVA) sizes of wing elements based on sex.

			MANOVA			MANCOVA		
Element	♀	♂	F	df	P	F	df	P
All			**2.53**	**13,22**	**0.026**	**2.66**	**12,22**	**0.022**
FA	60.33	58.41	0.60	1,34	0.445	**3.36**	**1,33**	**0.007*****
P1	15.68	15.22	0.37	1,34	0.550	0.02	1,33	0.638
P2.1	47.37	45.76	0.26	1,34	0.613	1.09	1,33	0.305
P3.1	57.52	55.40	0.36	1,34	0.554	0.01	1,33	0.905
P3.2	19.19	18.61	0.57	1,34	0.458	0.21	1,33	0.648
P3.3	30.85	29.69	1.30	1,34	0.263	1.03	1,33	0.318
P3.4	20.38	19.58	0.63	1,34	0.432	0.70	1,33	0.410
P4.1	56.62	54.63	0.06	1,34	0.804	1.15	1,33	0.292
P4.2	16.40	15.57	0.31	1,34	0.583	0.03	1,33	0.856
P4.3	22.68	21.58	**4.80**	**1,34**	**0.035**	**4.27**	**1,33**	**0.047**
P5.1	58.49	56.52	0.02	1,34	0.884	0.94	1,33	0.339
P5.2	12.90	12.56	1.89	1,34	0.178	1.28	1,33	0.266
P5.3	18.40	17.44	**15.32**	**1,34**	**<0.001**	**15.31**	**1,33**	**<0.001**

Table 2.—Quantitative characteristics of allometric relationships of wing elements with forearm length. r2 refers to the coefficient of determination of the relationship between forearm length and a particular wing element and P_1 refers to the significance of this relationship. b_1 refers to the regression coefficient for the relationship between forearm length and length of a particular element whereas P_2 refers to the probability that the observed b_1 is equal to unity.

Element	r2	P_1	b_1	P_2
P1	0.029	0.319	NA	NA
P2.1	**0.251**	**0.002**	**2.57**	**0.001**
P3.1	**0.432**	**<0.001**	1.22	0.315
P3.2	**0.183**	**0.009**	**2.55**	**0.005**
P3.3	0.028	0.332	NA	NA
P3.4	0.003	0.754	NA	NA
P4.1	**0.467**	**<0.001**	1.36	0.096
P4.2	**0.264**	**0.001**	**2.25**	**0.003**
P4.3	0.024	0.370	NA	NA
P5.1	**0.493**	**<0.001**	1.21	0.275
P5.2	**0.186**	**0.009**	**3.76**	**<0.001**
P5.3	<0.001	0.977	NA	NA


P1
P2.1
P3.2
P3.3
P3.1
P4.1
FA
P5.1
P4.2
P3.4
P4.3
P5.2
P5.3
FA- Forearm
P5.1- Fifth digit, metacarpal
P5.2- Fifth digit, first phalanx
P5.3- Fifth digit, second phalanx
P4.1- Fourth digit, metacarpal
P4.2- Fourth digit, , first phalanx
P4.3- Fourth digit, second phalanx
P3.1- Third digit, metacarpal
P3.2- Third digit, first phalanx
P3.3- Third digit, second phalanx
P3.3- Third digit, third phalanx
P2.1- Second digit, metacarpal
P1 – First Digit