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Craniometric diversity of the common vampire bat (*Desmodus rotundus*) in Central and South America

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The common vampire bat, *Desmodus rotundus* Geoffroy, 1810, is a species with an extensive geographical distribution, occurring in a wide variety of habitats. A recent phylogeographical study using molecular markers described a scenario in which this species is formed by 5 distinct geographically circumscribed mitochondrial clades. Here we studied the craniometric variation of the common vampire bat to assess the amount of subdivision within this species and to test for the possibility of distinct morphological patterns associated with geographical lineages. We used 16 measurements from 1,581 complete skulls of adult *D. rotundus* representing 226 localities in South America and Mesoamerica. The assessment of morphological diversity between groups was done by the estimation of minimum F_{ST} values. Overall, the results show that most of the within-species variation is a result of the size component. Both shape data and size data are correlated with geographic distances. Our results favor the origin of biological diversity as the outcome of genetic drift and stepping-stone pattern of gene flow instead of local adaptations to local environmental conditions. The F_{ST} analyses also support male-biased dispersal. The results give little evidence to support previous suggestions that the common vampire bat may be composed of 2 or more species.

Key words: craniometric diversity, *Desmodus*, Neotropics, vampire bat

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The study of geographical variation in natural species is one of the fundamental tools for understanding microevolutionary processes (Mayr 1963). Species with broad geographical distributions may comprise more than 1 operational taxonomic unit, and the study of geographical variation is vital so as to establish the geographical boundaries of each operational taxonomic unit (Moritz 1994) as well as to give insights into the historical processes responsible for the geographical distribution of the morphotypes (Avise 2000). The present morphological diversity of a species may be a product of adaptive responses to current and past physiographical attributes such as climate, vegetation, or elevation, or reflect stochastic evolutionary patterns due to population fragmentation (Caumul and Polly 2005; Malhotra and Thorpe 1997; Straney and Patton 1980; but see Collard and Wood [2001] and Mayer and Von Helversen [2001] for a critique against phylogenetic effects on cranial morphology). As a consequence, the study of the structure of morphological diversity of a species might bring important insights to its evolutionary history and dispersion pattern across its geographic distribution, complementing other sources of information (Caumul and Polly 2005; Straney and Patton 1980). In this article we present an assessment of the craniometric diversity of the common vampire bat, *Desmodus rotundus* Geoffroy, 1810, across Central and South America, comparing its morphological variability with previous molecular studies. Our main goal is to characterize the species' craniometric variability and contribute additional information to our understanding of the microevolutionary processes that shaped the present biological diversity *D. rotundus*.

Desmodus rotundus is a species with an extremely broad geographical distribution in Middle and South America: it ranges from southern Mexico to northern Chile in the west, and ranges over the entire territories of Brazil and Uruguay in the east (Greenhall et al. 1983; Koopman 1988; Kwon and Gardner 2007). Throughout its extensive range it occurs from sea level to over 3,500 m of elevation and has been captured in

habitats as diverse as rain forests and semiarid landscapes. It is believed that this species relies on either caves or forested areas for roosting, with the possibility of being captured in open sites while foraging (Martins et al. 2007).

The common vampire bat feeds exclusively on blood, preferentially from medium- to large-sized mammals (Greenhall 1988). It has been shown that this bat has a preference for domestic cattle as its main source of food (Voight and Kelm 2006). The common vampire bat lives in colonies that generally consist of fewer than 100 individuals (Sanpedro et al. 2008), and it has been suggested that females are phylopatric (Wilkinson 1988). The specific feeding strategy of *D. rotundus* is associated with important specializations of the skull, such as reduced numbers of teeth and lack of enamel on the teeth, which serves to maintain their sharpness. The morphology of *D. rotundus* is described as extremely conservative in long-term evolution, with variation within the genus being a product more of size differences than of shape variation (Lemen and Freeman 1984).

Probably because of its unique cranial and external morphological characteristics, there are very few taxonomic revisions in the literature regarding not only *D. rotundus* but the entire subfamily Desmodontinae. Since its original description (Geoffroy 1810), 8 additional descriptions of *D. rotundus* can be found in the literature. These descriptions were all listed as synonyms by Cabrera (1958). Osgood (1912) recognized 3 subspecies for this taxon. The 1st subspecies was nominated *D. r. rotundus*, ranging from the north of the Andes cordillera and the southern end of the Amazon to the southern limit of the species' distribution, with the holotype from Asunción, Paraguay. A 2nd recognized subspecies is *D. r. murinus*, the type locality of which is listed only as Mexico by Wagner (1840), and that ranges from Mexico in the north to the Amazon Basin in the south, including all of Central America and the island of Trinidad. The criterion adopted for delimiting these subspecies was overall body size. A 3rd subspecies, *D. r. dorbignyi*, was described based on the coloration of an individual from Chile, west of the Andes, but it was rejected by Cabrera (1958) on the basis that the color pattern described for this individual was present east of the Andes as well. In the most recent review of vampire bat systematics, Koopman (1988) acknowledged the existence of considerable morphological variation throughout the common vampire bat range, but proposed that this variation is not enough to warrant assigning subspecies status to any particular geographic population of *D. rotundus*.

Recent phylogeographic studies have revealed cryptic or previously undescribed species, or both, in Chiroptera, especially in species with a broad geographical distribution (see Mayer and Von Helversen 2001). Regarding *D. rotundus*, Martins et al. (2009) carried out a molecular phylogeographical study of the common vampire bat and described a scenario in which this species is formed by 5 distinct mitochondrial clades that became separated in the early to mid-Pleistocene, following forest dynamics associated with this period (Prance 1982). Each mitochondrial clade represents a distinct geographical lineage. The clades are the Central America clade; the Amazon and central Brazilian savannas clade (the Cerrado); the clade of the Pantanal and adjacent areas; and the northern and southern clades found within the Atlantic coastal forest of Brazil. Even though the exact evolutionary relationships between these 5 clades was not clear, the authors demonstrated that there was a sharp distinction between east and west in the Brazilian territory (i.e., between Atlantic Forest samples and the samples from the remaining landscapes), separated by the South American dry belt of xeromorphic formations. The mitochondrial marker analyzed by Martins et al. (2009) showed an unusually high degree of genetic divergence between these clades, strong evidence of historical fragmentation that indicates that *D. rotundus* might be composed of several different species according to the criteria outlined for the application of the Genetic Species Concept (see Bradley and Baker 2001).

Here, we describe how the craniometric variation of *D. rotundus* is structured in South and Central America, with the objective to check to what extent the molecular diversity reported earlier is reflected in the cranial morphology of the species and, consequently, describe the possible historical mechanisms producing the morphological differentiation among populations of *D. rotundus*.

Materials and Methods

The data used in this study consist of 1,581 complete skulls of adult *D. rotundus* representing 226 localities in South America and Mesoamerica. The complete list of specimens examined is available upon request directly to the authors. All specimens were measured by one of us (FMM) and 16 linear measurements were recovered from each specimen. All measurements included in this study follow the protocol presented in Vizzoto and Taddei (1973). Fig. 1 presents details on the variables measured. Because most of the localities are represented by only a few specimens, series were combined into groups that represent larger geographic regions. Group combination was made when a locality had fewer than 15 specimens. As a result, none of the groups considered here have fewer than 17 individuals, allowing for a fair representation of the geographic variation observed within each region. The geographic location of each of the combined groups as well as the geographic range of the series included in it are presented in Fig. 2. Groups were formed according to geographic proximity and environment proximity. However, this was not possible for the groups Brazilian Amazonian, Colombia, Ecuador, and Peru. Yet, in Brazilian Amazonian, all groups share the same biome, which has been continuous during the entire Holocene. In the remaining series, samples are geographically close, even if in some cases the localities belong to distinct formations. In all cases, however, the samples inside each group are very homogeneous, so that the series do not mask high intergroup differences. The geographic location of each combined series was calculated as the centroid of the polygon formed by the locations included in it.

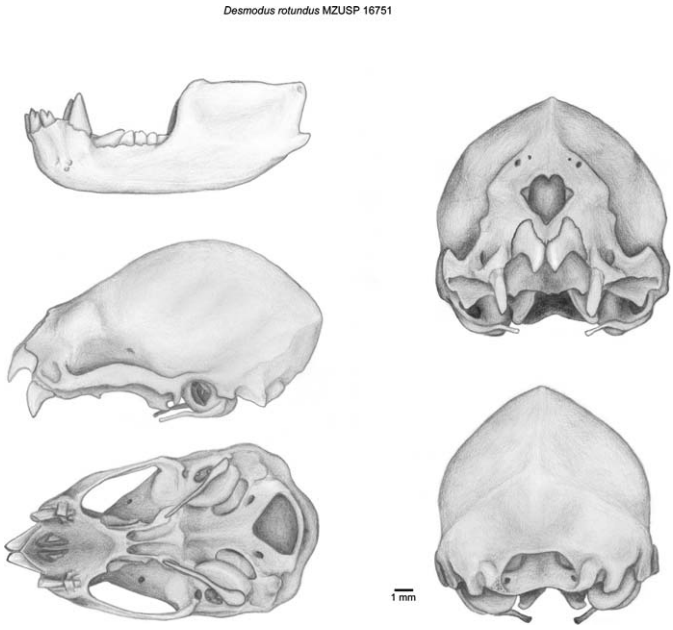

Fig. 1.—Lateral, ventral, frontal, and occipital views of a skull of *Desmodus rotundus* with measurements indicated; lateral view of mandible with measurement indicated. The measurement numbers and their descriptions are as follows: 1) length of the cranium; 2) length of cranium including incisors; 3) length from the alveolar border of the incisors to the mastoid; 4) length from the occipital condyle to the canine; 5) length from the canine to the opposed mastoid process; 6) basal length—from the posterior alveolar border to the border of the central incisors anterior to the incisive foramen; 7) length from the posterior alveolar border of the central incisors to the most anterior point of the palatine bone; 8) length from the nasal bones to the foramen magnum; 9) length of the mandible; 10) external width of the superior canines between the external points of the canines; 11) interorbital width—width between the points nearest the orbital constrictions; 12) preorbital width—width between the most proximal points of preorbital constriction; 13) width between the widest points of the cranium laterally, on left and right sides; 14) width between left and right mastoid processes; 15) height of the cranium—from the deepest point on the basicranium to the highest point of the parietal bone; 16) occipital height—from the anterior border of the foramen magnum to the highest point of the cranium.

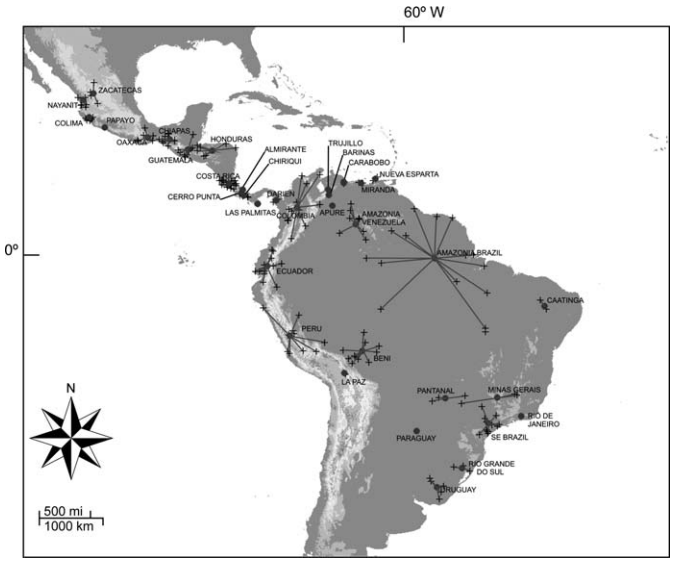

Fig. 2.—Sampled locations for *Desmodus rotundus* plotted on the map of Central and South America. Dots represent the location of the 11 combined groups, whereas the black crosses show location of local samples. Lines show which crosses were combined into each group and their geographic range.

Appendix I presents the coordinates of the series as well as the climate data recovered for each one.

The assessment of morphological diversity between groups was done by the estimation of minimum F_{ST} values (Relethford and Blangero 1990). F_{ST} values can be defined as the amount of the variation that is derived from between-group differences, and actually represent how much each groups' centroid deviates from the total group centroid (Relethford 1994; Relethford and Blangero 1990). Consequently, pairwise F_{ST} values can be used as a measurement of distance between groups, which considers the relationship of within-group and between-group variability (Roseman and Weaver 2004). F_{ST} values can be estimated from phenotypic data, as demonstrated by Relethford and Blangero (1990). However, F_{ST} values must be seen as minimum estimates (i.e., conservative estimates), unless the heritability of the phenotypic traits is known. Some studies have found that the heritability of craniometric measurements ranges from average to high in many organisms (Carson 2006; Cheverud 1988; Devor 1987; Leamy 1974), but there are no available data on this subject for bats. Here we use the minimum uncorrected F_{ST} values. This limits its direct comparison to molecular F_{ST} values, but does not invalidate its use as a measure of relative distance between groups, because any correction due to heritability would affect all pairwise F_{ST} values equally and does not change the relationship between them (Relethford and Blangero 1990).

Morphological relationship between the series was represented through neighbor joining trees (NJTs—Saitou and Nei 1987) based of the pairwise minimum F_{ST} values. NJTs was chosen here because it generates better phylogenetic trees than other methods in most simulations performed by Kim et al. (1993). Because most of the between-population differentiation within *D. rotundus* might be associated with size variation, all F_{ST} calculations and subsequent NJTs were made with 3 different data sets: the 1st with the raw material, the 2nd based only on the cranial size of the specimens, and the last based on size-corrected data. Size was estimated as the geometric means of all variables of each individual, and size-corrected data were obtained by dividing the original variables by the geometric mean (Darroch and Mosimann 1984; Jungers et al. 1995). We chose to calculate the geometric mean as a proxy to skull size instead of just removing the 1st principal component of the analysis for the following 2 reasons. First, by calculating the geometric mean we get a measure of size that can be studied independently from the shape variables. Second, despite the fact that size is responsible for a significant amount of the phenotypic variation of any species, and as such it is usually highly correlated with the 1st principal component, it cannot be assumed as the sole major source

Table 1.—The 36 groups composing the neighbor joining trees (NJTs) analysis were combined into 11 regions that included all groups sharing a similar ecological environment.

Regions	Groups within region	No. males	No. females	Total no.
Western Mexico	Zacatecas	50	85	135
	Nayani			
	Colima			
	Papayo			
Central America	Oaxaca	146	134	283
	Chiapas			
	Guatemala			
	Honduras			
Eastern Central America	Costa Rica	119	141	260
	Almirante			
	Cerro Punta			
	Chiriqui			
	Las Palmitas			
	Darien			
Amazonia	Miranda	151	168	324
	Carabobo			
	Nueva Esparta			
	Apure			
	Yaracuy			
	Venezuelan Amazonia			
	Brazilian Amazonia			
Northeastern Brazil	Caatinga	66	72	138
Southern Amazonia	Beni	14	13	36
Northwestern South America	Barinas	48	43	98
	Trujillo			
	Colombia			
Central southern Andes	Ecuador	25	33	60
	Peru			
	La Paz			
Central South America	Pantanal	29	21	50
	Paraguay			
Southeastern Brazil	Minas	83	70	161
	Rio de Janeiro			
	Southeastern Brazil			
South	Rio Grande do Sul	14	22	36
	Uruguay			

of variation that is influencing the decomposition of the variance–covariance matrix into eigenvalues and eigenvectors. In other words, by excluding the 1st principal component as a proxy for size, one is also removing important sources of variation in the groups studied along with size.

For the NJTs analyses, the 36 groups were further combined into 11 regions that include all groups sharing a similar ecological environment (Table 1). The reason for this further grouping of series is because series within a region show low pairwise F_{ST} values, and thus represent series closely related from a craniometric perspective. Also, the NJTs with 11 regions were easier to interpret, because of the overall low F_{ST} values obtained between groups (see ''Results'').

Because some degree of sexual dimorphism has been described in *D. rotundus*, with females being larger than males, we also compared F_{ST} values between sexes of each region. Here, the 11 regions were assumed as the analytical unit because the subdivision of groups into sex severely affected the sample size of some of them. However, for the groups that preserved enough sample size to be compared between sexes, results did not differ significantly from the ones presented here (data not shown). Minimum F_{ST} calculations were performed in Microsoft Excel (Microsoft Corporation, Redmond, Washington), through a Visual Basic Macro written by André Strauss (Max Planck Institute for Evolutionary Anthropology, Tübingen, Germany), who allowed its implementation here. NJTs were calculated in NTSYSpc 2.21c (Rohlf 2009). Significance of the F_{ST} values was accessed through 100 random permutations of the individuals in the data set. F_{ST} values obtained from the permutations were contrasted with the observed F_{ST} and the significance level was assessed as the probability that the random combination of individuals resulted in a higher F_{ST} value than the one obtained for the original data. Permutations also were calculated using an Excel Visual Basic Macro, written for this purpose by MH.

Finally, to test if the morphological relationships observed here result from a neutral evolutionary differentiation process or adaptation to environmental changes, we correlated the pairwise F_{ST} values with different geographic and environmental variables. We calculated 5 distance matrices (linear geographic distance, altitude differences, mean annual temperature differences, annual precipitation differences, and relative humidity differences) and compared those with the pairwise F_{ST} matrix. The geographical coordinates for each locality were taken directly from the museum tags affixed to the specimens or through the use of a global gazetteer online (www.fallingrain.com/world). Linear geographic distances were calculated considering the approximate circumference of the earth. Distances ignored major geographic barriers such as the ocean or the Andes, because they did not considerably alter the relationships of the pairwise geographic distances. In our study, the Andes were not considered as a strong geographic barrier because of the lack of clear morphological differences between series from either sides of the cordillera. Alternatively, if we assumed that the Andes acted as a strong geographic barrier, this would add a bias to the geographic distance matrices resulting in overestimating the geographic distances between east and west series in relation to the north to south variation. Morphological change that is positively correlated with geographic distance is interpreted to be a result of neutral processes of evolutionary differentiation. Although a better way to test this would be to test the correlation between morphologic and molecular data directly, we chose not to do this here because the geographic coverage of the molecular data (Martins et al. 2009) is substantially poorer in comparison to the morphologic data used here, and would limit us to only 5 of the 11 regions included in this study.

The climatic distances were calculated from data retrieved for each coordinate from the WorldClim database (Hijmans et al. 2005) through DIVA-GIS version 7.1.7 .2 (http://www.diva-gis.org). The climatic values for each group can be found in Appendix I. Mantel matrix correlations tests (Mantel 1967) were performed between the pairwise F_{ST} matrix and each of the geographic and climatic predictor matrices. Mantel

Table 2.—Minimum F_{ST} values obtained between all 36 groups and mean pairwise F_{ST} values between groups of each region.

	Raw data	Size-corrected data	Size
36 groups	0.104579	0.08292	0.293762
Mean pairwise $F_{ST} \pm SD$ of groups within each region			
Western Mexico	0.062 ± 0.048	0.051 ± 0.033	0.090 ± 0.085
Central America	0.023 ± 0.011	0.022 ± 0.011	0.025 ± 0..023
Eastern Central America	0.051 ± 0.023	0.050 ± 0.023	0.027 ± 0.032
Amazonia	0.057 ± 0.043	0.048 ± 0.031	0.136 ± 0.175
Northeastern Brazil[a]	—	—	—
Southern Amazonia[a]	—	—	—
Northwestern South America	0.024 ± 0.002	0.020 ± 0.004	0.013 ± 0.013
Central southern Andes	0.032 ± 0.011	0.030 ± 0.012	0.035 ± 0.032
Central South America	0.054	0.056	0.034
Southeastern Brazil	0.062 ± 0.034	0.057 ± 0..028	0.063 ± 0.049
South	0.037	0.039	0.023

[a] Pairwise F_{ST} values are not available because these regions are composed of only 1 series.

correlations with 10,000 permutations were performed in NTSYSpc 2.21c (Rohlf 2009). Similar to the NJTs analyses, Mantel correlations were performed on 3 different data sets: raw data, size variables, and size-corrected data.

Results

The overall minimum F_{ST} values for the 36 groups for each of the 3 data sets and the mean pairwise F_{ST} values between series that were included in each of the 11 ecological regions are given in Table 2. As can be seen, minimum F_{ST} values are relatively low for both raw data and size-corrected data, with roughly 10% of the variation being explained by differences between groups. Size, on the other hand, presents high F_{ST} values, with almost 30% of its variation explained by intergroup differences. Overall, these results favor previous studies that show that most of the within-species variation in Yangopterochiroptera (sensu Teeling et al. 2005) is a result of the size component (Dzeverin and Ghazali 2010; Lemen and Freeman 1984).

Despite the fact that most of the within-region pairwise comparisons showed significant *P*-values (Table 2), all pairwise comparisons within regions present F_{ST} values below the F_{ST} observed when all groups are considered, showing that the largest between-group morphological differentiation occurs outside the geographic regions defined here. In other words, by grouping the series in the 11 geographic regions defined here, we are not masking large morphological differences between the series. This is especially true when only size is analyzed, and supports the grouping into ecological regions and also supports previous findings that suggest that ecological constraints are important sources of biological structuring in Yangopterochiroptera (Dzeverin and Ghazali 2010; Martins et al. 2007, 2009).

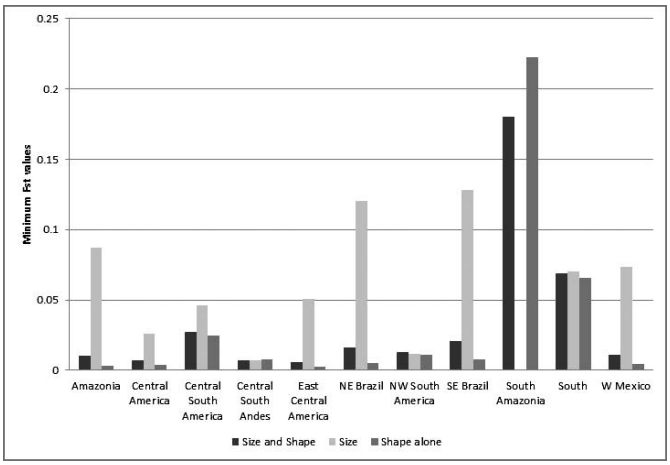

Fig. 3.—Minimum F_{ST} values obtained for each region for *Desmodus rotundus*.

Figure 3 shows the F_{ST} comparisons between sexes for each ecological region. It can be observed that, with the exception of South Amazonia (the Bolivian province Beni), most of the morphological dimorphism is a function of size, with females being larger than males, as also described in other studies (Delpietro and Russo 2002; Gomes and Uieda 2004; Mann and Aulagnier 1993). The differences seen in southern Amazonia are difficult to explain. Not only is the major difference within sex associated with shape, but also there is no variation in size explained by between-sex differences. Analyses of variance performed for each of measurements show that sexual dimorphism is associated with differences in measurements 2 (total length of the skull; $P = 0.048$) and 8 (nasal–foramen magnum interval; $P = 0.013$), which indicates that there is an important difference in skull length between males and females for this locality.

Figure 4A shows the NJTs obtained for the analysis of raw data for the total population and each of the sexes separately. There is a general consensus in the 3 NJTs obtained, with a clear division separating series from Central America and northern and northwestern South America from series from the central, southeastern, and southern part of the continent, in accordance with the molecular results obtained by Martins et al. (2009). However, some differences can be seen when sexes are analyzed separately. Northeastern Brazil and central Andes appear associated with the northern cluster in females, whereas for males they are associated with the southern cluster.

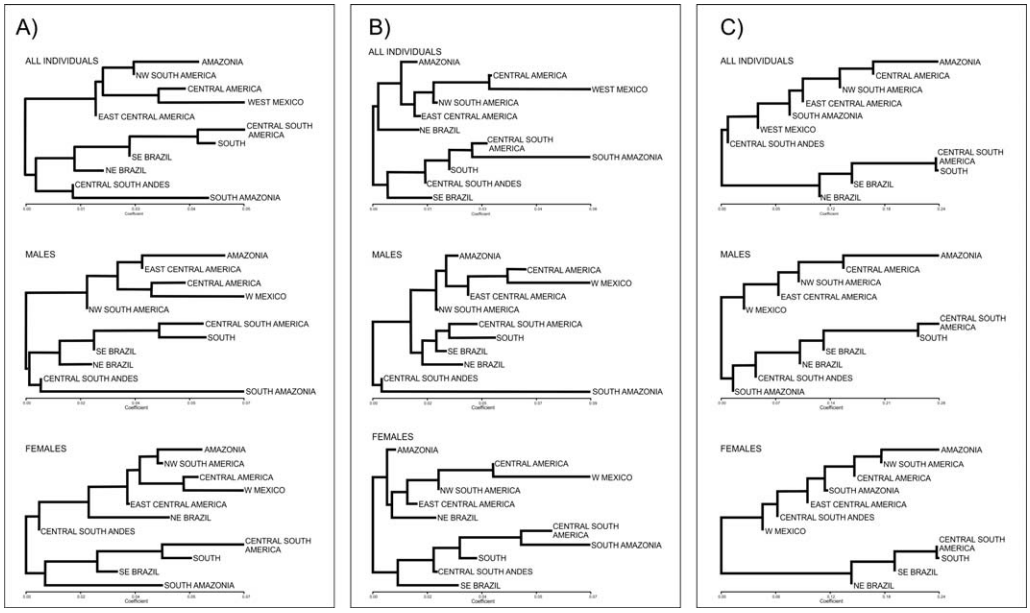

FIG. 4.—Neighbor joining trees showing the morphological relationships among the series of *Desmodus rotundus* according to pairwise minimum F_{ST} estimates. A) Raw data; B) size-corrected data; and C) size.

The same analyses for the size-corrected data are presented in Fig. 4B. The general trend of the north versus south division is still represented in all the NJTs obtained. Again northeastern Brazil and central Andes shift their association inside each of these major clusters, depending on sex. However, for this data set, male analyses show central Andes and Bolivian Amazonia as outliers to the 2 major clusters. With the exception of this last NJT, in all analyses Bolivian Amazonia appears associated with the southern cluster, which would appear to be evidence against the idea that the major structure of biological diversity is an east–west separation associated with the dry belt that separated the Amazon Forest from the Atlantic Forest during the Pleistocene (Martins et al. 2009).

Figure 4C shows the NJTs when only size of the individuals is considered. Size presents the greatest apportionment of the total variation due to between-group differences ($F_{ST} = 0.29$) and the trees obtained present a clearer structure. Size is correlated with latitude ($r = -0.67$; $P < 0.01$), with individuals being larger in southern populations. Nonetheless, the NJTs obtained also reflect the same division in 2 major clusters representing northern versus southern groups. Different from the analyses that considered shape, here northeastern Brazil is always associated with the southern cluster, whereas it is central Andes and Bolivian Amazonia that change their relationships depending on the sex being studied.

Finally, Table 3 presents the results of the correlations between pairwise F_{ST} values and each of the geographic and climatic parameters. Results are identical regardless of the data set used. The only parameter that shows significant correlations with the morphological distances is linear geographic distances among the series. Linear distance between series explains between 12% and 19% of the morphological variation ($r^2 = 0.12$–0.19; Table 3) observed between groups. The remaining climatic parameters show no correlation with distances between groups, indicating that environmental plasticity (at least with respect to the parameters tested) does not appear to explain the pattern of morphological diversity in *D. rotundus*. Because geographic distance can be a proxy for the differentiation associated with random microevolutionary processes such as drift (Harvati and Weaver 2006; Relethford 2004), these results give support to the resemblance observed between previous molecular data (Martins et al. 2007, 2009) and the present morphological affinity analyses of *D. rotundus*.

DISCUSSION

Yangopterochiroptera in general and *D. rotundus* specifically have been described as having conservative morphology, with slow rates of differentiation, partially due to their specialized alimentary habits (Freeman 2000; Gunnell and Simmons 2005). Morphological variation also has been explained as a result of changes in size rather than in shape (Lemen and Freeman 1984). Our results clearly support this description. When craniometric shape is considered, the apportionment of variation explained by between-group differences is only around 10% ($F_{ST} = 0.08$ for size-corrected data and $F_{ST} = 0.10$ for the raw data). Although this is based on minimum F_{ST} estimates (i.e., real F_{ST} would be higher if we corrected for traits' heritability), it shows that differentiation between populations is small, even smaller when we consider the mean pairwise F_{ST} values within each ecological region (Table 1). On the other hand, the apportionment of size variation due to between-group differentiation is considerably higher, around 30% ($F_{ST} = 0.29$), showing size alone to be the major source of differentiation in actual populations of *D. rotundus*.

Table 3.—Correlations between pairwise minimum F_{ST} values and geographic and climate distances.

Variable	Raw data	Size-corrected data	Size
Linear geographic distance			
r	0.427	0.437	0.350
r^2	0.183	0.191	0.123
P	0.0001	0.0001	0.0001
Mean annual temperature	0.049	−0.042	0.085
r			
r^2	0.002	0.002	0.007
P	0.2828	0.3746	0.1803
Annual precipitation	0.0332	0.065	−0.028
r			
r^2	0.001	0.004	0.001
P	0.3416	0.2325	0.4176
Altitude	−0.092	−0.066	−0.081
r			
r^2	0.009	0.004	0.006
P	0.2097	0.3114	0.2457
Mean relative humidity	0.028	0.092	−0.073
r			
r^2	0.001	0.008	0.005
P	0.3508	0.1809	0.2391

However, even though between-population variation is low, the diversity seen in the species is geographically structured. Both shape data and size data are correlated with geographic distances and the NJTs all show a major division between regions from Central America and northern South America and regions from central and southern South America. This pattern of organization does not follow the distribution of subspecies' description (Osgood 1912), but is in accordance with mitochondrial DNA (mtDNA) genealogical lineages (Martins et al. 2009), being also a strong indicator that the main factor responsible for differentiation within *D. rotundus* is isolation by distance. In other words, our results favor the origin of biological diversity as the outcome of genetic drift and stepping-stone pattern of gene flow instead of being due to local adaptation to local environmental conditions.

Although the NJTs show some inconsistencies regarding the morphological relationships between geographical regions, especially regarding the central Andes, northeastern Brazil, and Bolivian Amazonia regions, the major clusters found in every analysis have a strong correspondence to the molecular phylogeographic pattern published by Martins et al. (2009). As in the case of mtDNA phylogeography, there seems to be a clear east-west distinction in the Brazilian territory (see Fig. 4). Thus, the pattern between genetic and morphological systems seems to be very similar. In a study of a possible historical connection between the Amazon and the Atlantic Forest, Costa (2003) showed that the gallery forests of central Brazil acted as a corridor where distinct intraspecific mtDNA lineages from the Amazon Forest and the Atlantic Forest meet. In the case of the common vampire bat, the samples from central Brazil analyzed by Martins et al. (2009) were clustered in the Amazon and central Brazilian savannas clade. In the case presented here, the skulls from central Brazil and from Bolivian Amazonia have a closer affinity with the ones from the Atlantic Forest and the southern grasslands near the southern limit of the species' distribution. This result shows the importance of central Brazilian gallery forests as a historical contact zone for populations separated by the South American dry diagonal. If there has been gene flow mediated by gallery forests in central Brazil between east and west populations, then the admixture between these populations in central Brazil could generate individuals with mtDNA haplotypes from the Amazon region but with morphology more similar to that of the coastal region, as described in this study.

Craniometric features are inherited from both parents. In the work of Martins et al. (2009), a clear geographic structure was described for the mtDNA marker (which is maternally inherited), but for the 2 nuclear DNA markers used in the same study there was no phylogenetic structure, only significant F_{ST} values, as described here. In some bat species (see Castella et al. 2001), dispersal is biased toward males. In the common vampire bat, females are considered philopatric and Martins et al. (2009) could not distinguish between male-biased dispersal and incomplete lineage sorting for the nuclear markers. The results presented here support the hypothesis that male-biased dispersal is likely responsible for the pattern observed in nuclear DNA markers and cranial features.

Another issue regarding the comparison between molecular and morphological findings is the existence of large sampling gaps, especially in the molecular study. Because of the relatively course geographic sampling in the molecular studies, the hypothesis of isolation by distance could not be completely discarded by Martins et al. (2009), except for the Brazilian Atlantic Forest. Even though our cranial data also have clear sampling gaps in similar areas as the previous phylogeographic study, it is likely that better sampling would reinforce the results obtained here instead of bringing novel insights, because the opposite ends of the distribution are covered.

In our analyses, we find no substantial ground to justify the subspecies recognized by previous researchers. The subspecies recognized by Osgood (1912) are based on the size of the specimens. *Desmodus* bats from the Amazon Basin and Central America are in fact smaller and weigh considerably less than specimens from other regions (F. M. Martins, pers. obs.). Koopman (1988) also pointed out the fact that specimens from Paraguay toward the southern end of the distribution were larger than their northern counterparts, which also is supported by our results. Additionally, the molecular data do not support the existence of the subspecies proposed by Osgood (1912) because the mitochondrial clades detected by Martins et al. (2009) are not congruent with these subspecies groups. Similarly, despite the geographic organization of craniometric diversity, examination of our data does not show any abrupt morphological discontinuities between ecological regions, which does not support the suggestion made by Martins et al. (2007) that the common vampire bat may be composed of 2 or more species.

Resumo

O morcego vampiro comum, *Desmodus rotundus*, é uma espécie de ampla distribuição geográfica, que ocorre em uma variedade de habitats. Um recente estudo filogeográfico baseado em marcadores moleculares descreveu um cenário onde a espécie é formada por 5 linhagens distintas, geograficamente circunscritas. Neste estudo, se apresenta a variação craniométrica deste morcego para descrever o seu grau de subdivisão intra-específico e testar a existência de linhagens geograficamente distintas. As análises consideraram 16 medidas lineares provenientes de 1,581 crânios de espécimes adultos de *D. rotundus*, representando 226 localidades das Américas do Sul, Central e do Norte. A avaliação da diversidade morfológica entre grupos foi realizada através da estimativa de valores mínimos de F_{ST}. Os resultados mostram que a maior parte da variação intraespecífica resulta de diferenças em tamanho. Além disso, forma e tamanho dos crânios estão significativamente correlacionados com distância geográfica. Estes resultados sugerem que deriva genética e isolamento por distância são a explicação mais parcimoniosa para o processo que deu origem a diversidade morfométrica em *D. rotundus*. Os resultados não corroboram estudos anteriores que defendem que o morcego vampiro comum seja formado por duas ou mais espécies.

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Appendix I

Sample size, geographic coordinates and climatological and locality variables for each geographical location (group).

Groups	Sample size	Latitude (°)	Longitude (°)	Elevation (m)	Mean temperature (°C)	Annual precipitation (mm)	Relative humidity (%)
Almirante	19	9.30	−82.40	27	25.90	2,867	79
Brazilian Amazonia	64	−0.39	−55.47	344	25.70	2,159	77
Venezuelan Amazonia	114	4.44	−66.52	108	27.50	2,973	80
Apure	28	7.04	−69.85	105	27.30	1,793	80
Barinas	21	8.50	−70.30	313	26.40	1,996	78
Beni	36	−13.42	−65.60	143	26.30	1,491	78
Caatinga	138	−7.08	−40.00	400	25.50	745	64
Carabobo	51	10.21	−68.20	215	26.00	1,206	77
Cerro Punta	32	8.85	−82.56	508	23.80	3,154	82
Chiapas	150	16.35	−92.71	575	23.80	1,233	76
Chiriqui	22	8.42	−82.27	241	25.60	3,318	84
Colima	41	19.45	−104.05	2,208	15.60	1,216	63
Colombia	38	6.75	−74.78	1,015	22.80	2,925	84
Costa Rica	100	10.13	−84.34	1,473	18.80	3,217	85
Darien	24	7.81	−77.72	294	25.20	2,830	85
Equador	37	−1.43	−78.96	2,005	15.70	1,498	85
Guatemala	33	14.91	−90.12	827	23.00	980	80
Honduras	45	14.80	−86.74	941	22.10	1,221	75
La Paz	33	−16.55	−68.11	4,499	4.60	629	59
Las Palmitas	26	7.30	−80.30	48	26.80	1,821	82
Minas	24	−19.96	−46.61	1,145	19.40	1,564	76
Miranda	29	10.23	−65.76	21	27.70	1,281	76
Nayarit	33	21.94	−104.90	286	24.00	1,571	79
Nueva Esparta	19	10.81	−63.80	2	27.60	346	78
Oaxaca	55	16.59	−95.81	1,031	21.00	1,148	56
Pantanal	24	−20.02	−53.95	538	23.70	1,479	72
Papayo	19	18.00	−101.81	557	25.50	891	71
Paraguay	18	−24.68	−57.95	79	23.20	1,014	69
Peru	27	−11.28	−75.77	3,456	10.00	670	64
Rio Grande do Sul	18	−29.82	−51.58	87	19.40	1,385	77
Rio de Janeiro	17	−22.53	−43.23	390	21.00	1,953	83
Southeastern Brazil	120	−23.59	−47.88	637	19.20	1,172	77
Trujillo	39	9.32	−70.38	617	24.60	1,163	78
Uruguay	26	−32.56	−55.12	103	17.70	1,217	72
Yaracui	19	10.36	−68.20	215	26.00	1,206	77
Zacatecas	42	22.80	−103.45	2,093	16.10	477	53