

## Chapter 4

## GENETICS

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## I. INTRODUCTION

Aside from their obvious mythical appeal, vampire bats, as a result of their specializations for obligate blood feeding, have received much attention from researchers interested in morphological and physiological adaptations of mammals (for review see Turner<sup>42</sup> and Altenbach<sup>1</sup>). The same anatomical features which reflect specializations for sanguivory have also made the phylogenetic assessment of vampire bats both difficult and controversial. Although there is general agreement that vampire bats share a sister-group relationship to other New World leaf-nosed bats in the family Phyllostomidae,<sup>29,15,44</sup> some researchers prefer to allocate the three extant genera of vampire bats to a separate family Desmodontidae,<sup>29,43</sup> whereas others place the vampires as a subfamily Desmodontinae within the family Phyllostomidae.<sup>15,22,21</sup>

Most genetic oriented research on vampire bats has a strong evolutionary basis and focuses primarily on phylogenetic relationships with respect to various subfamilies within the Phyllostomidae as well as the relationships among the three genera, *Desmodus*, *Diaemus*, and *Diphylla*. Recently, population level genetic variation has been examined in *Desmodus rotundus* with respect to the effects of sociality on genetic variability and divergence.<sup>46</sup> This review will focus primarily on the genetics of vampire bats with respect to systematic relationships and the patterns and processes of genetic change. Genetic characters used to date have been chromosomes and molecules; thus, these will be the primary data discussed.<sup>15,20</sup> We evaluate these data in light of proposed phylogenies of vampire bats, interpretations of chromosomal and molecular evolution, and where appropriate, ideas for future genetic research.

## II. CHROMOSOMAL VARIATION

### A. Nondifferentially Stained Karyotypes

Nondifferentially stained karyotypes of vampires were published and reviewed by Cadena and Baker<sup>10</sup> and Baker.<sup>5</sup> *Desmodus* has a diploid ( $2n$ ) number of 28 and a fundamental number ( $F_n$  = number of arms present in the autosomal complement) of 52, whereas *Diaemus* and *Diphylla* both have a  $2n = 32$  and an  $F_n$  of 60, although it is obvious from the morphology of the chromosomes that *Diaemus* and *Diphylla* do not have identical karyotypes. A more detailed analysis of chromosomal variation is provided by G- and C-banding of the individual chromosomes.<sup>6</sup>

### B. C-band Variation

C-bands provide a means of determining the distribution of highly repetitive DNA in the karyotype. The distribution of C-band positive material (= highly repetitive DNA) is considered significant because it identifies which chromosomal rearrangements have resulted in changes in the euchromatic linkage groups (= DNA involved with single copy genes). In *Desmodus* and *Diphylla*, C-band positive material is restricted to the centromeric regions, and in *Diaemus* there are C-band positive regions both at the centromeres and also on some of the telomeres. However, all chromosomal arms have a definite euchromatic portion. Although there is minimal variation to amounts of C-band positive DNA in the genomes of the various species of vampires, studies on the origin and significance of the telomeric heterochromatin in *Diaemus* may be valuable in understanding how the repetitive sequences evolved during bat evolution.

### C. G-band Variation

In contrast to C-bands, G-bands (Figures 1 to 3) provide a means of estimating genetic homology of euchromatic arms through comparisons of patterns of bands that are distin-

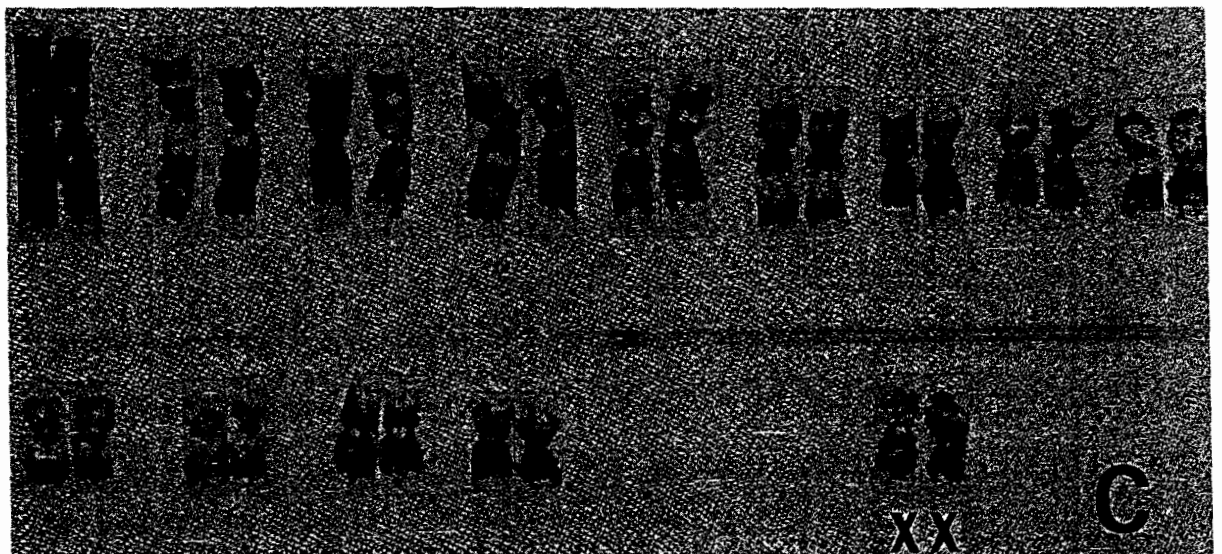
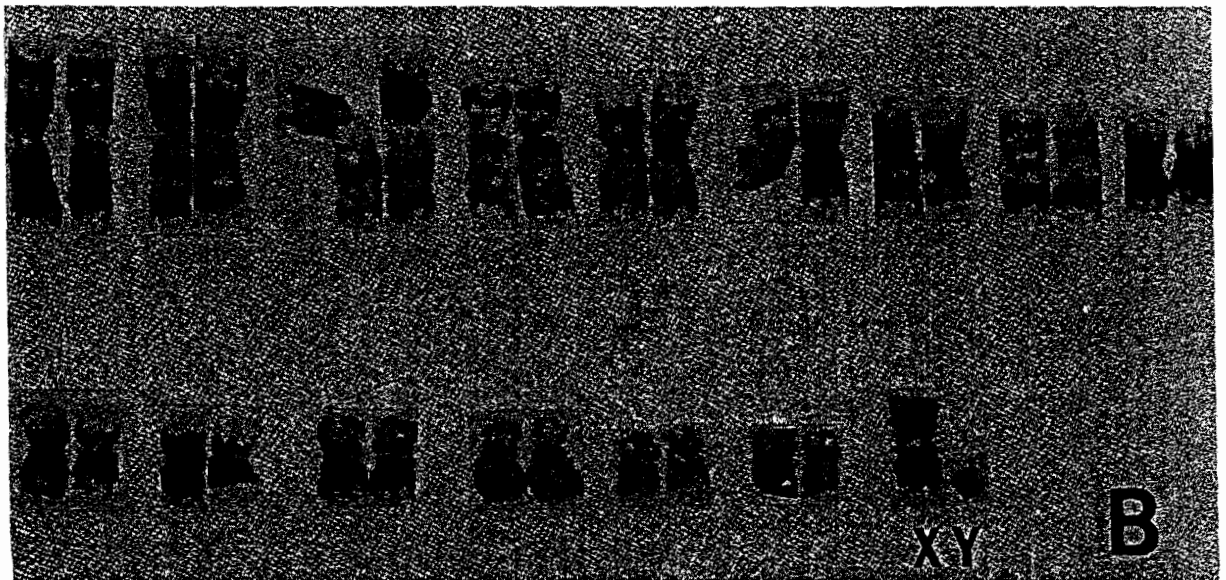
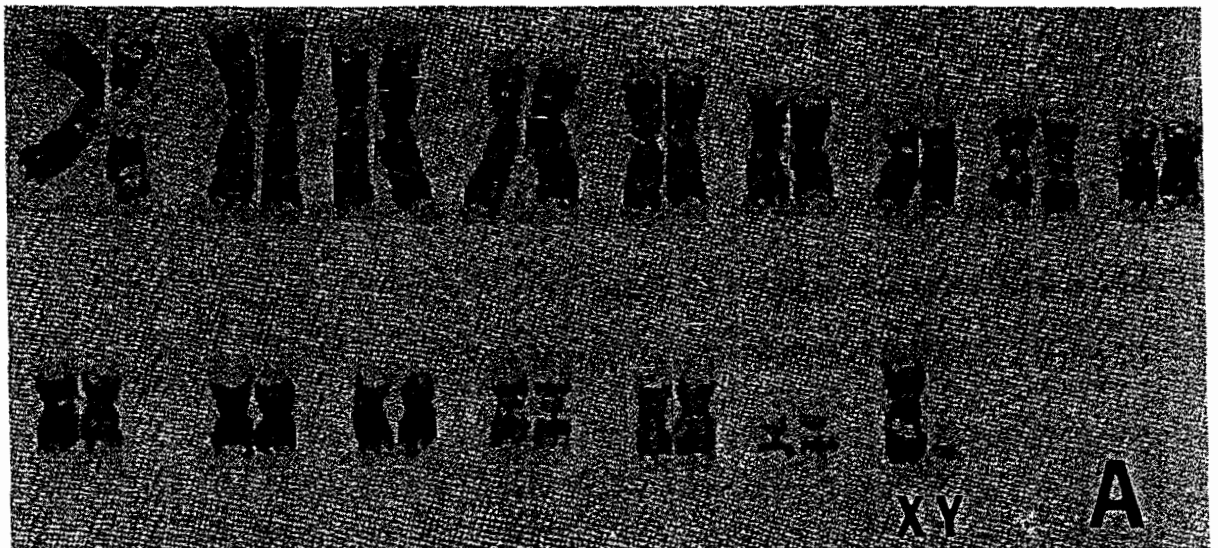


FIGURE 1. (A) Representative G-banded karyotype of *Diaemus youngii*. (B) Representative G-banded karyotype of *Diphylla edaudata*. (C) Representative G-banded karyotype of *Desmodus rotundus*.

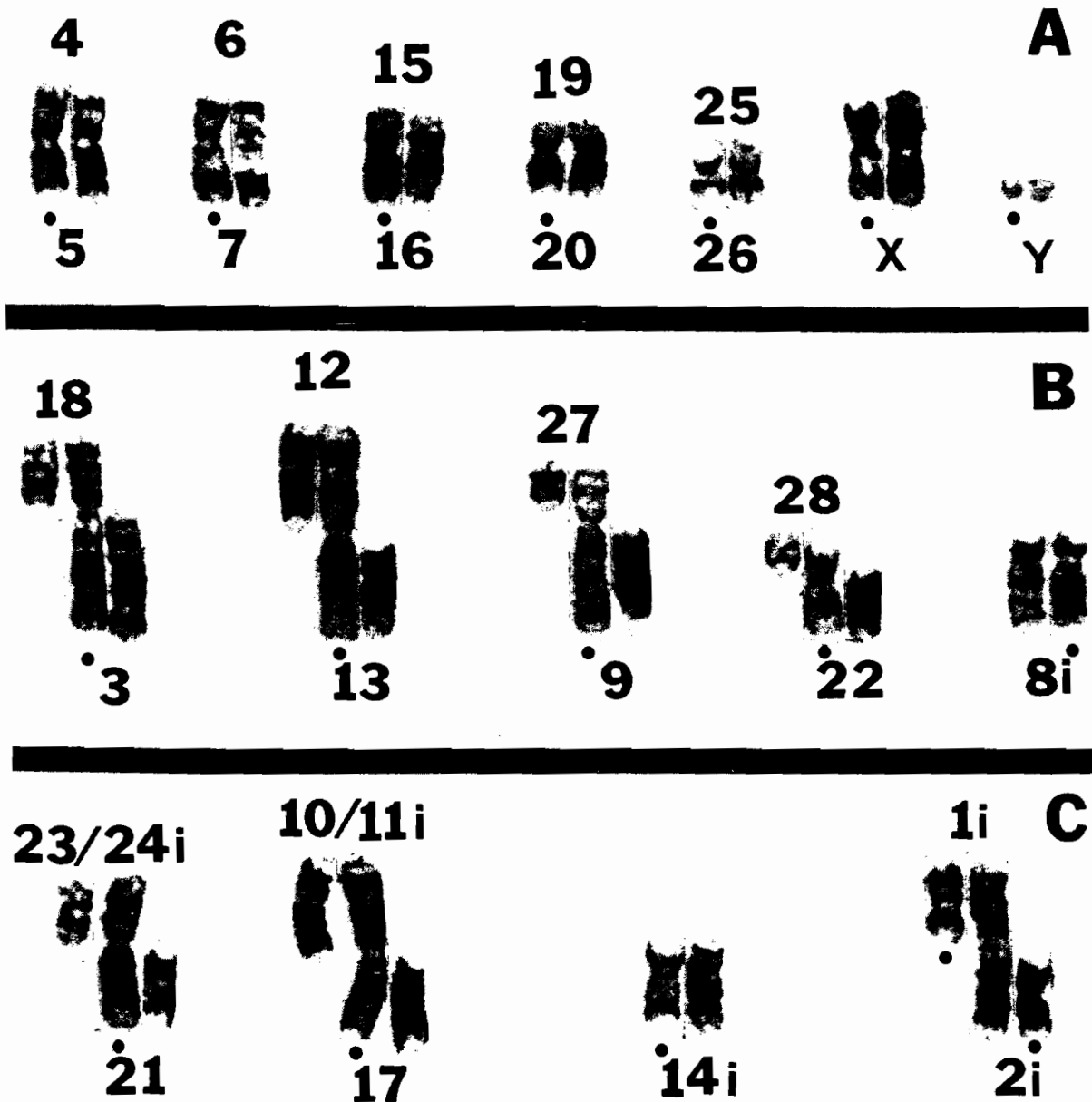


FIGURE 2. Haploid G-banded chromosomes of *Diaemus* compared to those of *Macrotus waterhousii*. For each proposed homologous comparison, the chromosomes of *Diaemus* are identified by a dot. Row (A) represents biarmed elements proposed as primitive for all phyllostomid bats and that are unchanged in the karyotype of *Diaemus*. Rows (B) and (C) are chromosomes that are rearranged from the proposed primitive karyotype for phyllostomid bats.

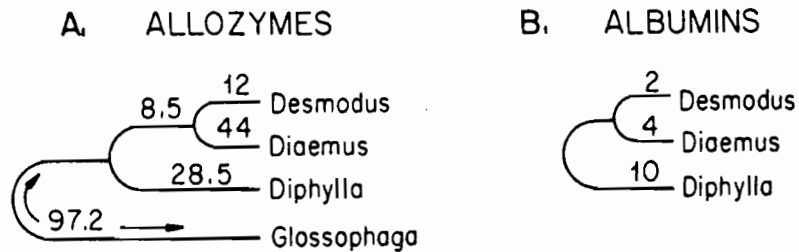


FIGURE 3. Proposed evolutionary relationships of the three species of vampires. (A) Using allozymes based on starch-gel electrophoresis, using *Glossophaga* as an outgroup. (B) Using immunological distance from the albumin molecules.

guished by differential staining intensity. (See Baker et al.<sup>6</sup> and Haiduk and Baker<sup>17</sup> for comments on estimating genetic homology from G-bands). Results from our analysis of G-bands suggest that each of the three species of vampires share considerable chromosomal homology and that a number of chromosomal arms can be related among the three species of vampires as well as to other phyllostomids and the mormoopids and noctilionids.

Patton and Baker<sup>32</sup> proposed a primitive karyotype for the Phyllostomidae. Our analysis indicates that the karyotype of *Diaemus* is most unchanged from that proposed as primitive. In the proposed primitive karyotype there are eight biarmed pairs, and in *Diaemus* 5 of these pairs (4/5, 6/7, 15/16, 19/20 and 25/26) are unchanged. Of the three remaining pairs, two (10/11 and 23/24) appear to have undergone an inversion producing an acrocentric which has been translocated to another acrocentric. The final biarmed pair (1/2) appears to have undergone a centric fission, producing two acrocentrics, both of which were inverted into biarmed elements. In the proposed primitive karyotype there are 14 acrocentric pairs. Two of these pairs (8 and 14) appear to have been inverted into biarmed elements, while eight pairs (tentatively identified as 3, 9, 12, 13, 18, 22, 27, and 28) have undergone centric fusions resulting in four biarmed pairs. Two acrocentrics, probably the 17 and 21, are fused to the inverted 23/24 and 10/11 mentioned above. No element was found that appeared like acrocentric pair 29.

Some caveats are in order, as there are too few bands on some of the chromosomes to positively identify some elements and undoubtedly some misidentification has occurred; however, we feel most arms have been properly identified.

Variation among the vampires appears to be associated with chromosomal pairs tentatively identified as 8i, 15/16, 19/20, 22, 28, 25/26; however the solution to all chromosomal change cannot be provided at this time.

In an overview, the types of chromosomal change associated with vampire evolution involves translocations (both centric fusions and other more complex types) and inversions. Additionally, *Diaemus* has added some C-band positive material to the telomeric regions of some chromosomes.

### III. BIOCHEMICAL GENETICS

#### A. Divergence

The two experimental techniques used in studies of the biochemical genetics of vampire bats have been starch gel electrophoresis of enzymatic and nonenzymatic protein and quantitative immunology involving microcomplement fixation.<sup>41,20,46</sup> Both approaches can be used to produce estimates of genetic divergence which provide indirect inference as to the number of amino acid substitution differences (with respect to particular proteins) which separate different taxa, populations or even individuals. In terms of starch gel electrophoresis, differences reflect charge changes in a particular molecule as a result of the replacement of amino acids differing in charge.<sup>37</sup> Immunology, on the other hand, involves the assessment of surface changes in the molecule as detected by antigen-antibody cross-reactions.<sup>12</sup> The common measurements of genic (electrophoretic) divergence or similarity are Nei's D,<sup>31</sup> and Rogers' S,<sup>35</sup> respectively. Immunological difference is reported as immunological distance units with one unit being approximately equivalent to one amino acid substitution.<sup>32,36</sup> All the above measurements have been reported in studies involving vampire bats.

#### B. Genic Variation Within *Desmodus rotundus*

Patterns of genic variation within *Desmodus rotundus* have been examined throughout a portion of this species' geographic distribution. A brief comment concerning this variation was provided in Honeycutt et al.<sup>20</sup> and we will now present a more detailed account of our findings.

Twenty-two presumptive loci encoding 15 enzymatic and one nonenzymatic proteins were examined for patterns of genic variation within *Desmodus* using horizontal starch gel electrophoresis.<sup>20</sup> Variation was assessed in 42 individuals collected from Mexico (Queretaro, n = 10), Guatemala (Santa Rose, n = 3), two localities in Honduras (Valle, n = 2; Morazan, n = 5), three localities in Nicaragua (Zelaya, all near Rama, n = 3, 3, and 4), and two localities in Costa Rica (San Jose, n = 10; Puntarenas, n = 2). Of these 22 loci, 6 (Est-1 and 3, Icd-1, Sod-2, Pgi-1, and Pgm-1) were polymorphic with average proportion of loci polymorphic per population ( $\bar{P}$ ) ranging from 9 to 23%. Nicaragua ( $\bar{P}$  = 23%) and Costa Rica ( $\bar{P}$  = 18%) had the highest level of polymorphism, which probably reflects (at least in part) larger sample sizes. By far the most variable loci which revealed two or more alleles were the esterases (Est-1 and 3) and sorbitol dehydrogenase (Sod-2). Observed levels of heterozygosity (H) were highest in Nicaraguan (4.8%) and Costa Rican (4.4%) populations, with the overall level of heterozygosity being approximately 3%.

Genetic similarity values (Rogers' S), for all pairwise comparisons between *Desmodus* populations, averaged 0.98. From the standpoint of geographic variation as reflected by genic similarity, *Desmodus* populations are rather homogeneous with little genic variation within or between populations. This observation (at least indirectly) is concordant with the fact that few trinomens have been recognized throughout the range of this species.<sup>11</sup>

### C. Sociality and Genetic Differentiation in *Desmodus*

The level of genic homogeneity as seen from a geographic perspective and overall patterns of variation agree well with the recent findings of Wilkinson.<sup>46</sup> Although five of the seven polymorphic loci reported by Wilkinson were not examined in our study, two of the polymorphic loci observed by Wilkinson (Icd and Est) were found to be polymorphic in our Costa Rican samples with one Icd-1 allele occurring only in Mexican and Costa Rican *Desmodus*. Of more general interest with respect to our study was that Wilkinson's study involved an assessment of allozymic variation in *Desmodus* which was designed to evaluate the amount of genic variation within and between groups of vampire bats from several roost sites in a localized region of Costa Rica. The fact that vampire bat females are known to share common roosts and display reciprocity with respect to regurgitated blood being shared between related and unrelated individuals, suggests that a relatively complex social system exists for vampire bats.<sup>45</sup> Wilkinson's allozymic study, together with behavioral observations allowed him to address the relationship between genetic subdivision and the expression of certain types of social behavior. The overall findings of Wilkinson were that there was a low level of genetic relatedness within female roosts and little genetic differentiation between roosts, although female offspring are recruited into natal groups.<sup>46</sup> Wilkinson explained this lack of genetic heterogeneity by the facts that males disperse, females occasionally move between groups; and there is a high infant mortality, and adult mortality is low. Thus the characteristics of dispersal and infant mortality prohibit the form of sociality seen in vampire bats from promoting genetic differentiation between roosts.

The study by Wilkinson and similar studies on *Phyllostomus hastatus* provide empirical data which help explain not only the apparent panmixia observed from the geographic analysis of *Desmodus*, but also dispel any simplistic association of sociality to population subdivision, increased inbreeding, and incipient speciation as advocated by some authors.<sup>9,27,28,46</sup> These studies also reveal the value of using genetic markers in behavioral studies where some idea of relatedness is necessary in order to evaluate social interactions between individuals. Both the *Desmodus* and *Phyllostomus* studies are social systems which merit further research. Genetic markers derived from restriction endonuclease analysis of mitochondrial DNA (mtDNA) would provide valuable information on certain matrilineal relationships within particular roosts. As suggested by Wilkinson,<sup>46</sup> several matrilineal lines exist within a roost of *Desmodus* as a result of female movement, but the frequency of such movement and the

relationships of individuals with respect to matriline can only be determined by observation over many years where the population turnover of individuals can actually be observed or indirectly inferred using a limited number of allozymic markers.<sup>46</sup> Mitochondrial DNA is maternally inherited and provides a useful marker for determining the number and members of a particular matriline, and in addition, the molecule evolves at a rate which is fast enough to insure a considerable amount of variation at the population level.<sup>3,8,4,24</sup> Future studies involving the use of additional molecular markers will increase our knowledge of the unique social systems and life history strategies associated with extreme adaptations such as sanguivory.

#### IV. SYSTEMATIC RELATIONSHIPS

##### A. Intergeneric Relationships of Vampire Bats

Aside from Cadena's systematic study on vampire bats which concentrated more on intrageneric relationships and less formally on intergeneric relationships, there is a general lack of conclusive morphological evidence which directly addresses phylogenetic relationships among the three species of vampire bats, *Desmodus rotundus*, *Diaemus youngi*, and *Diphylla ecaudata*.<sup>11</sup> Several authors have suggested that *Desmodus* and *Diaemus* are morphologically more similar to each other than either is to *Diphylla*.<sup>29,38,39,16,11</sup> Two informal taxonomic treatments suggest that *Diaemus* and *Desmodus* are congeneric, with *Diphylla* representing a separate genus.<sup>18,23</sup> The problem of all the morphological studies to date is that a detailed character analysis and cladistic treatment of morphological characters diagnostic for relationships among the three vampire bat genera is lacking. The characters used for systematic arrangements are primarily those which are important adaptations for sanguivorous feeding (such as loss of cheek teeth), and inasmuch as it is probable that the three vampire genera shared a common sanguivorous ancestor, accumulation of further morphological refinement would be expected in independent lineages. It is therefore difficult to determine if such characters as the loss of teeth in *Desmodus* and *Diaemus* occurred in a common ancestor or represent convergent events resulting from trends in adaptive morphology.

Our approach to addressing the intergeneric relationships of the vampire bats has been to derive phylogenetic associations among the three genera using two molecular techniques, starch gel electrophoresis and albumin immunology.<sup>20</sup> The allozymic data for the three genera of vampire bats consisted of 17 presumptive loci, and these data were analyzed phenetically using distance data (Nei's D) and a locus-by-locus cladistic analysis.<sup>20</sup> The relationships resolved from both approaches can be seen in Figure 3. The phenetic analysis using the Fitch and Margoliash<sup>14</sup> method of tree construction and *Glossophaga* as the outside reference species reveal a closer relationship between *Diaemus* and *Desmodus* relative to *Diphylla*. This relationship did not change when other genera (*Sturnira*, *Brachyphylla*, *Erophylla*, and *Phyllonycteris*) were used to root the tree. If one examines the amount of change along individual lineages, almost four times the amount of change has occurred along the *Diaemus* lineage. Such rate destabilization of molecular evolution is characteristic for phyllostomid bats in general.<sup>2,19</sup> The locus-by-locus cladistic analysis reveals the same relationships with two synapomorphies (Idh-1<sup>c</sup> and Idh-1<sup>d</sup> alleles), supporting the *Diaemus* and *Desmodus* association. Again, fewer apomorphies were seen along the *Desmodus* lineage, suggesting a slower rate of change relative to *Diaemus*.

The immunological analysis of albumin immunological distances among the three genera of vampire bats also support a *Desmodus* and *Diaemus* association (Figure 3b). Unlike the electrophoretic distances (Nei's D) between (*Diaemus* and *Desmodus*, the immunological differences between these two genera are small, relative to most intergeneric albumin immunological distances.<sup>13,36</sup>

Overall, the molecular data support a common ancestry of *Desmodus* and *Diaemus* after

separating from *Diphylla*, as suggested in earlier morphological treatments. However, such a close relationship for *Desmodus* and *Diaemus* is not evident from a cladistical analysis of the G-banded chromosomes. Whether *Desmodus* and *Diaemus* are congeneric is not clearly defined from the genetic data. If one considers only magnitude of change, the molecular data are not equivocal in that allozymically all three genera are quite divergent, whereas immunologically *Desmodus* and *Diaemus* appear to be as closely related as most species within other genera of mammals. Obviously, magnitude of change is not the only criterion to use in making a taxonomic decision in this case (or possibly any case), and we suggest that any taxonomic change should come from a more comprehensive study (including classical morphology, molecules, chromosomes, etc.) of vampire bats relative to other phyllostomids in general.

### **B. Familial Associations of Vampire Bats**

The specialized nature of vampire bats for obligate feeding on blood has led certain systematists to consider these bats as representing a distinct family, Desmodontidae. On the other hand, morphological data unrelated to feeding habit strongly suggest an alignment of vampire bats within the family Phyllostomidae.<sup>25,15,22</sup> The cladistic analysis of female reproductive histomorphology by Hood and Smith<sup>22</sup> document several synapomorphies which associate vampire bats with phyllostomid bats, in general, as members of a larger monophyletic group. These authors do suggest that vampires represent a clade that diverged relatively early in phyllostomid evolution.

The phylogenetic relationship of phyllostomid bats has been examined in detail using albumin immunology, and the results of these studies provide direct information relative to the phylogenetic associations of vampire bats.<sup>19,21</sup> A phenetic analysis by Fitch and Margoliash<sup>14</sup> of albumin immunological distances agree with the histomorphological data in that the vampire bats represent an early offshoot of the phyllostomid radiation. The vampires relative to other bat reference points (such as the mormoopids and noctilionids) are clearly part of the phyllostomid monophyletic group. Recent transferrin immunological distance data also support the vampires as part of the phyllostomids.<sup>33</sup> There are some contradictions, however, between the albumin and transferrin data. Based on albumin immunology, the vampires are linked with the *Macrotus* lineage. This association is not supported by the morphological or chromosomal data. Given the unusual rate of destabilization seen in albumin evolution within phyllostomoids, the association of vampires and *Macrotus* may be the result of equally divergent albumins relative to other phyllostomid albumins.<sup>2,19</sup> The transferrin data agree with the albumins in the fact that the vampires are seen as an early offshoot of the phyllostomid radiation, but do not support the association with *Macrotus*.<sup>33</sup> Thus, the association of vampires and *Macrotus* as a result of albumin rate changes seems to be supported by the transferrin data.

The affiliation of vampire bats within the Phyllostomidae is clear from immunological, morphological, and chromosomal data. To consider the vampires as a separate family obscures the evolution of sanguivory and constructs an unnatural classification.

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