RESOLVING A PHYLOGENY WITH MULTIPLE DATA SETS: A SYSTEMATIC STUDY OF PHYLLOSTOMOID BATS

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All comparative biological data (in this study morphological, chromosomal, electrophoretic, and immunological) ultimately must be interpretable within a specific framework—the actual phylogeny of the set of organisms under study. An obvious corollary is that each data set should contribute toward the delineation of that phylogeny. The quality and magnitude of contribution, of course, will vary with the nature of the data set and its mode of evolution, because two conditions are necessary. First, a change must have occurred along the lineage under study and second, evidence of change must be observable.

In this study, we were concerned with delineating phylogenetic relationships among the three families of New World bats currently placed in the superfamily Phyllostomoidea—Noctilionidae (one genus, two species), the Mormoopidae (two genera, eight species), and the Phyllostomidae (some 49 genera and approximately 139 species). In addition, we have examined intrafamilial associations in the Noctilionidae and the Mormoopidae.

The genera Mormoops and Pteronotus classically have been placed either in the family Mormoopidae or (formerly) in the subfamily Chilonycterinae within the family Phyllostomidae. The systematic association of Mormoops with Pteronotus, suggesting a shared common ancestor for these genera following their separation from all other taxa in the superfamily, has been recognized since the work of Dobson (1875). Noctilio, on the other hand,
clearly has presented more of a problem to chiropteran systematists. Some workers have associated Noctilio with the Emballonuroidea (Dobson, 1875; Trouessart, 1897; Miller, 1907; Simpson, 1945), whereas others (Winge, 1892; Smith, 1972; Patton and Baker, 1978) have indicated a mormoopid-phyllostomid association for these bats.

Chromosomal change between the Mormoopidae and Noctilionidae constitutes the least amount of divergence thus far documented between two mammalian families (Patton and Baker, 1978). Chromosomal data have been interpreted as supporting a common ancestry for the two families (five synapomorphic elements present) and for the two mormoopid genera (one synapomorphic element present—Patton and Baker, 1978), with two rearrangements distinguishing Mormoops from Pteronotus (Baker and Bickham, 1980).

In order to understand better the evolution of the superfamily Phyllostomoidea, we have reviewed the resolving power and systematic value of classical comparative anatomy, karyology (using G- and C-banding techniques), electrophoresis of various proteins, and albumin immunology. Furthermore, we have evaluated the extent to which each of the above analyses contributes to the delineation of an internally consistent phylogeny.

**Materials and Methods**

**Electrophoretic Analyses**

All samples were assayed for 18 isozymes. The enzyme and protein systems were malate dehydrogenase-1 and 2 (Mdh-1,2), phosphoglucomutase-1 and 2 (Pgm-1,2), lactate dehydrogenase-1 and 2 (Ldh-1,2), isocitrate dehydrogenase-1 and 2 (Idh-1,2), α-glycerophosphate dehydrogenase (α-Gpd), leucine aminopeptidase (Lap), peptidase (Pep), phosphoglucose isomerase-1 and 2 (Pgi-1,2), glutamate oxalate transaminase-1 and 2 (Got-1,2), indophenol oxidase (Ipo), albumin (Alb), and hemoglobin (Hb). Tissue preparations, staining procedures, and enzyme designations followed those of Selander et al. (1971).

For examination of electrophoretic data, populations (see list of specimens examined for numbered localities) 1-7 (Pteronotus parnellii), 8-9 (Pteronotus davyi), 12-13 (Pteronotus personatus), 15-16 (Mormoops megalophylla), and 18-20 (Noctilio leporinus) were grouped according to species. A cladistic analysis was performed on the data set by using the electromorphs as independent character states (Hennig, 1966). The two species of Noctilio represented
an outgroup comparison for *Pteronotus* and *Mormoops* in the
electrophoretic study. Any allele present in both *Noctilio* and spe-
cies of *Mormoops* and *Pteronotus* was considered primitive for the
two families. Further resolution of phylogenetic relationships,
based on electrophoretic data, was made possible by using the iso-
zyme systems for which no primitive allozyme was distinguishable
from the outgroup comparison. This involved examination of the
polarity of allozymic variation, with the assumption that the most
common electromorph was primitive for the mormoopid-
noctilionid clade and that all other variants were derived. The
results from the use of this technique did not involve the rear-
rangement of any relationships defined by the outgroup process;
rather, they further refined relationships involving previously
undefined lineages.

*Immunological Analyses*

The albumins of *Mormoops megalophylla, Pteronotus parne-
litii,* and *Noctilio leporinus* were purified according to the tech-
niques of Cronin and Sarich (1975). Antisera to these albumins
were prepared in rabbits (three to four Dutch Belted rabbits per
albumin according to the schedule of Sarich, 1969), and each
individual antiserum then was titered using microcomplement
fixation (MCF) and pooled in reciprocal proportion to its titer
(Sarich and Wilson, 1966). Additionally, two antisera pools to the
albumins of phyllostomid bat genera (*Macrotrus, Vampyrurus,
Glossophaga, Carolia,* and *Desmodus*) and pteropid bat genera
(*Syconycteris, Pteropus, Dobsonia, Nyctimene,* and *Paranycti-
mene*) were used to provide estimates of the amounts of albumin
change along the *Mormoops, Pteronotus,* and *Noctilio* lineages,
as well as to test for relationships to the phyllostomids. All anti-
gens used for cross-reactions with the different antisera were
extracted from samples of whole serum or tissue diluents.

Immunological cross-reactions (antigen-antibody reactions) for
all comparisons were measured by the quantitative precipitin
technique employed by Sarich and Wilson (1966) and Prager and
Wilson (1971). The degree of cross-reaction was expressed quan-
titatively as albumin immunological distance units (AID), with
one unit being approximately equivalent to one amino acid sub-
stitution (Prager and Wilson, 1971; Maxson and Wilson, 1974).

**Specimens Examined**

Specimens used in this study were collected at the following localities: *Pterono-
utus parnellii.*—1) 1 km. N Mérida, Yucatán, México, 2 females; 2) Guatopo
National Park, Santa Crucita Campground, Venezuela, 2 females, 1 male; 3) 1 mi. N El Dorado, Sinaloa, México, 3 males; 4) 2 mi. NE Rosario, Sinaloa, México, 1 male; 5) 0.4 mi. E Hwy. 15 on road to Acapone property, Nayarit, México, 1 male; 6) 24.1 mi. N Río La Unión on Hwy. 200, Guerrero, México, 1 male; 7) 0.2 mi. E Watermount, Jamaica, 16 females, 5 males; *Pteronotus davyi.*—8) 15 km. N Altgracia de Orito, Guatrico, Venezuela, 1 female; 9) Tanetane, St. John Parish, Dominica, 7 females, 10 males; *Pteronotus macleayii.*—10) St. Clair Cave, St. Catherine Parish, Jamaica, 15 females, 5 males; *Pteronotus quadridens.*—11) St. Clair Cave, St. Catherine Parish, Jamaica, 11 females, 10 males; *Pteronotus personatus.*—12) Tehuantepec, Oaxaca, México, 5 males; 13) El Fuerte, Sinaloa, México, 1 male; *Mormoops blainvillii.*—14) St. Clair Cave, St. Catherine Parish, Jamaica, 20 males; *Mormoops megalophylla.*—15) 24.1 mi. N Río La Unión on Hwy. 200, Guerrero, México, 1 female; 16) 8.2 mi. S Piña Blanca on Hwy. 120, Querétaro, México, 2 males; *Noctilio albiventris.*—17) 15 km. N Altgracia de Orito, Guatrico, Venezuela, 1 female, 1 male; *Noctilio leporinus.*—18) 0.2 mi. E Watermount, St. Catherine Parish, Jamaica, 5 females, 3 males; 19) mouth of Belham River, St. Anthony, Montserrat, 3 females, 4 males; 20) 1 mi. above mouth of Layou River, St. Joseph Parish, Dominica, 1 female.

**RESULTS AND DISCUSSION**

**Electrophoretic Analyses**

Only one isozyme (Lap) was monomorphic for all populations (Table 1). Nine of the remaining 17 isozyme systems yielded information concerning primitive and derived conditions using the outgroup criteria. The cladogram represented by Fig. 1 was produced by first using the data from these systems and then further resolving relationships based on the remaining allelic data as discussed in the section on methods. Allozymes present in the internodes (for example, Got-11^136^) are synapomorphic for the species located above the internode, whereas allozymic characters located on branches ending in a single species (for example, Idh-1^160^) are considered autopomorphies for that species.

Several phylogenetic relationships are suggested from the cladistical analysis of electrophoretic data (Fig. 1). First, a clade composed of the five *Pteronotus* species is defined by four synapomorphic electromorphs. Within that assemblage, *P. parnellii* is separated from the other four species by the Idh-1^133^ and Got-1^156^ allozymes.

The two species of *Mormoops* and the two of *Noctilio* are united by three and seven shared characters, respectively, with all of these electromorphs belonging to loci for which the outgroup criteria failed to discriminate primitive and derived conditions.
Table 1. Allozyme data for the 20 populations of mormoopid and noctilionid bats (see text for identification of numbered populations). The mobility of the most frequent allozyme in population 2 was arbitrarily designated 100 with all other allozymes being designated relative to this electromorph. A negative (−) sign indicates a cathodal mobility of the allozymes, whereas the lack of any sign indicates anodal mobility.

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Morphological Analyses

Smith (1972) analyzed the morphological relationships between the families Mormoopidae, Noctilionidae, and Phyllostomidae as well as the inter- and intrageneric relationships of mormoopid taxa. Although Smith's study was basically phenetic in its approach, he did evaluate a large array of qualitative characteristics, not only for the Phyllostomoida but also for other New World Chiroptera. This set of data is unique for bats in that it provides an adequate base for cladistic analysis. Fig. 2 represents our interpretation of these qualitative characters, a description of which appears in the legend. In deriving the cladogram, we assumed that emballonuroids represent a valid outgroup.

The resolved phylogenetic tree (Fig. 2) presents several salient features. The families Phyllostomidae, Mormoopidae, and Noctilionidae share several synapomorphies and represent a unified clade, as suggested by Smith (1972). However, a closer association of the Noctilionidae to the Mormoopidae than to the Phyllostomidae is not demonstrable. Although the Mormoopidae and Noctilionidae share a single derived character, a synapomorphic ele-
Fig. 1.—Cladogram based on allozymic variants. Allozymes denoted by asterisk were resolved using the outgroup method. See text for identification of abbreviations.

ment also is present between the families Phyllostomidae and Mormoopidae. One synapomorphy places the genera Mormoops and Pteronotus together; another (shape of tragus) separates P. parnelli from its congeners, with the other four species of Pteronotus forming an unresolved tetrotomy. One and three synapomorphic characters, respectively, unites the species of Noctilio and Mormoops.

**Karyotypic Analyses**

Chromosomal data as presented by Patton and Baker (1978) and Baker and Bickham (1980) add additional resolution to phylogenetic relationships within the Phyllostomoidae (Fig. 3). The primitive karyotype for the superfamily, as proposed by Patton and Baker (1978), consists of a 2n=46 and FN=60, essentially the karyotype of the phylllostomid species Macrotrus waterhousii. Based on the assumption that the 2n=46, FN=60 karyotype is primitive for the Phyllostomoidae, the families Noctilionidae and Mormoopidae are linked by five synapomorphies (Robertsonian fusions). Patton and Baker (1978), using the rule of parsimony, indicated that the
fusion events probably were synapomorphies inasmuch as several more events, including fissions preceded by several fusions, would have to be invoked to explain a noctilionid-mormoopid-like karyotype as primitive. A cladistic analysis to determine a primitive karyotype for the Phyllostomoidoidea cannot be performed at this time because homologous elements have not been identified with appropriate outgroups. Mormoopid and noctilionid species differ by four rearrangements (Patton and Baker, 1978)—a fission event in the mormoopids (synapomorphic for Mormoops and Pteronotus) and an inversion, a fusion event, and a heterochromatic addition in the noctilionids (synapomorphic for the two Noctilio species). Additionally, Mormoops blainvillii differs from the species of Pteronotus by a paracentric inversion and a heterochromatic addition (Baker and Bickham, 1980).

**Immunological Analyses**

A salient feature of almost all phyllostomoid albumins is their immunological distinctiveness relative to those of other bats. The assumption of microchiropteran monophyly or the use of phylogenetic analyses involving nonbat reference species (Sarich, unpublished data) leads to the conclusion that an event producing
Table 2.—Albumin immunological distance values for mormoopid and vucuilloid species. The Phylllostomidae sample is a mixed outgroup consisting of Macrotus, Vampyrum, Glossophaga, Carollia, and Desmodus. The Pteropodidae sample consists of Syconycteris, Pteropus, Dobsonia, Nyctimene, and Paranyctimene.

<table>
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<th>P. p.</th>
<th>V. L.</th>
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the antigenic equivalent of 30 to 40 units of albumin immunological distance must have occurred early in phylllostomid history (Table 2, Fig. 4). Thus, this event has provided an effective phyletic marker that positions a wide variety of New World bats into a single clade. It also would appear that such an event has caused a relative rate destabilization for subsequent albumin evolution in the group (at least as it is assessed immunologically). There is appreciably more variation in observed amounts of change along different lineages than has been demonstrated in any other vertebrate group (Honeycutt and Sarich, unpublished data). It thus is fair to point out that the “molecular clock” concept never would have been formulated on the basis of a study of phylllostomid albumin evolution. This does not, however, affect our cladistic analysis, as the data for phylllostomid bats apportion into additive phylogenies at least as well as do those for any other group for which similar information is available. For example, the F value (Prager and Wilson, 1978) for the input-output comparisons involving 16 phylllostomid albumins and antisera to them is less than 5 per cent (Honeycutt and Sarich, unpublished data).

As systematists, we find it disturbing that the cladistical analysis of data from albumins of Mormoops are not consistent with the results of similar analyses of morphological and chromosomal data. Mormoops, Pteronotus, and various phylllostomid albumins are more or less equidistant from one another. Indeed, if anything, the albumins of the two mormoopid genera are, on the average, somewhat more distant from each other than either is from albumins of the phylllostomids. However, we would have expected, given the usual association of Mormoops and Pteronotus on the basis of anatomical similarities, to find that their albumins had changed to a greater degree than those of the phylllostomids. Otherwise, the albumin data would not be readily interpretable within the generally agreed upon framework that
represents mormoopids as a derived unit relative to other bats. Yet we find that the least-changed albumin in this set is that of Mormoops megalophylla, at a distance of 140 units from our pteropodid reference set, whereas Pteronotus barnellii is 178 and the phyllostomid mean is 172 (Table 2). These data may be explained most parsimoniously by suggesting that the phyllostomids and Pteronotus shared a common ancestor (separate from Mormoops) in which there was an albumin change of approximately 30 or so AID units (Fig. 4)—in other words, a second event of similar magnitude as that proposed to have occurred in the common ancestral stock of all phyllostomoid bats.

Noctilio is still another problem immunologically. Its albumin is divergent in the same way as that of other phyllostomoids, being some 180 units from those of the pteropodids (Table 2). It is also quite different from those of other phyllostomid lineages with which we are concerned. The distances separating Noctilio from Pteronotus, Mormoops, and an assortment of phyllostomids are 150, 146, and 135 units, respectively (Table 2). The cladistic implications of these data are not unequivocal. For example, the apportionment of the Noctilio-phyllostomid distance of 135 units, using the pteropodid information, would suggest a Noctilio separation somewhere along the common phyllostomid lineage to which we have allocated a singular conformation-altering mutation (Fig. 4). Subsequent to that separation, it is then evident that this “event” was completed in a somewhat different fashion along
the Noctilio line relative to what happened along the Pteronotus-
phylllostomid line, thus resulting in a markedly divergent albumin.

*Albumin Irregularities*

Over the last 15 years, extensive evidence has been developed
that documents the generally time-dependent nature of immuno-
logically assessed albumin evolution. However, significant indi-
vidual departures from this pattern do exist in that a few lineages
among many have accumulated change at a rate significantly
greater or less than the average. Examples are Aotus, Caluromys,
Marmosa, and Ursus on the slow side, and Rousettus and Phaner
on the fast side (Sarich, 1969; Cronin and Sarich; Maxson et al.,
1975). Of course, such a lineage ultimately could develop into a
major adaptive radiation leading to a large clade, all the individu-
ual lines of which might appear removed from clocklike behavior;
one such instance already has been reported (Cronin and Sarich,
1975). In that particular case, it appears that at some time along
the ancestral anthropoid lineage, subsequent to the anthropoid-
prosimian split, about 25 to 30 units of change in excess of the
average accumulated. Almost all anthropoid albumins thus
appear to be changed to a greater degree than do those of most
prosimians. Although this could be regarded simply as twice the
usual rate of change over the period of time involved (about 50
million years), the rate being normal before and after, it is appre-
ciably easier to envision it as resulting from a single mutation
that somehow altered the conformation of the albumin surface so
as to be the antigenic equivalent of many individual amino acid
substitutions.

There is excellent evidence that the number of differences in the
surface amino acid sequence between two native proteins can be
closely approximated by quantitative immunological comparisons
(reviewed in Wilson et al., 1977), although alterations of the three-
dimensional structure can have drastic effects. One can imagine,
therefore, a single internal amino acid substitution (perhaps
involving a cysteine and the subsequent relocation of one or more
disulfide bridges) that could have a similar effect on the three-
dimensional protein structure on a reduced scale. One also might
interject a cautionary note here concerning the possible nonequi-
valence of immunological distances derived from conformational
changes and those derived from the accumulation of single amino
acid substitutions. We include this as a final note for considera-
tion of albumin evolution in phyllostomoid bats, where more than the usual number of interpretive problems exist.

**Character State Evolution and the Derivation of Phylogenies**

As witnessed by a continuing list of authors (Mickey and Johnson, 1976; Schnell et al., 1978; Turner, 1974), the derivation of a consistent (that is, congruent) phylogeny using different character states is, to say the least, complicated. Is a similar method of analysis (cladistics) the key to deriving congruent phylogenies? Consistency seems achievable if one adequately can interpret patterns of character state divergence in terms of a similar method of analysis that potentially can detect differential rates of change, degree of homoplasy, and primitive (as opposed to derived) conditions. The cladistical method seems appropro; however, regardless of the method of analysis, certain limitations inherent to a particular type of character may limit congruence (Fig. 5). In our data sets, limitations for different character states can be categorized as follows: 1) In terms of morphology, chiropteran systematics is still at a stage where evolutionary relationships are based mainly on a "gestalt," due in part to the lack of a fossil record. An appropriate quantitative approach (void of size relationships) to morphological relationships within chiroptera does not exist. The qualitative approach used in our study does support the phyllostomoid superfamilial association; however, the associations among the three families as well as those between Mormoops and Pteronotus are much more tentative (Figs. 2 and 5). 2) The electrophoretic approach is limited by inability to resolve synapomorphic character states among the genera Mormoops, Pteronotus, and Noctilio (Fig. 1). 3) The chromosomal approach is limited because of our current inability to decipher chromosomal homologies between superfamilies and thus to determine conclusively (without the rule of parsimony) primitive conditions at superfamilial levels (Figs. 3 and 5). 4) Phylogenetic associations such as those implied with albumin immunological data are clearly more accurate in cases where divergence can be correlated to surface amino acid substitutions. Structural changes of the albumin molecule only can be inferred and at this stage in scientific investigations are not usually verifiable (Table 2).

The inconsistent resolving power associated with a given suite of characters indicates that the best phylogeny generated from different types of characters need not reflect total congruence. Rather, an alternate consideration would be one of compatibility.
Fig. 5.—Composite cladogram indicating the levels of resolution of each of the character sets used: A=albumin, C=chromosomal, E=electrophoretic, and M=morphological.

Every character does not have to resolve the same branching sequences at different evolutionary levels; however, all characters should lead to maximum compatibility. The failure of certain characters to resolve branching sequences at a given level then can be regarded as neutral insofar as determination of a consistent phylogeny. Incompatibility occurs only when different characters
reveal conflicting branching sequences. One is then forced to assess this incompatibility in terms of the characters used and the inconsistencies and limitations associated with those characters (see immunological discussion).

Our study supports the conclusion that a complex phylogeny can be resolved best by the use of multiple, differentially resolving character sets.

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