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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 species 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 isozyme 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 rearrangement 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 parnellii,* and *Noctilio leporinus* were purified according to the techniques 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 (MC'F) and pooled in reciprocal proportion to its titer (Sarich and Wilson, 1966). Additionally, two antisera pools to the albumins of phyllostomid bat genera (*Macrotus, Vampyrum, Glossophaga, Carollia,* and *Desmodus*) and pteropoid bat genera (*Syconycteris, Pteropus, Dobsonia, Nyctimene,* and *Paranyctimene*) 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 antigens 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 quantitatively as albumin immunological distance units (AID), with one unit being approximately equivalent to one amino acid substitution (Prager and Wilson, 1971; Maxson and Wilson, 1974).

Specimens Examined

Specimens used in this study were collected at the following localities: *Pteronotus 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 Acaponeta, 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 Altagracia de Orituco, Guarico, 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 Altagracia de Orituco, Guarico, 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-1^{156}) are synapomorphic for the species located above the internode, whereas allozymic characters located on branches ending in a single species (for example, Idh-1^{100}) are considered autapomorphies 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.*

	Population										
Isozyme	1	2-7	8-9	10	11	12	13	14	15-16	17	18-20
Mdh-1	100	100	100	100	100	100	100	34	44	138	138
Mdh-2	−100	−100	−107	−100	−100	−100	−100	−100	−100	− 89	− 89
Pgm-1	100	100(0.98) 30(0.02)	100	100	100	153	153	153	153	153	153
Pgm-2	−100	−100	−100	−129	−100	−100	−100	−100	−100	−100	−100
Ldh-1	100	100	100	100	100	100	100	126	82	147	147
Ldh-2	−100	−100	−100	−100	− 89	−100	−100	100	−100	−100	−100
Idh-1	100	100	133	133(0.42) 171(0.58)	133	133	133(0.50) 95(0.50)	114	164	114	114
Idh-2	−100	−100	− 62	− 38	−108	−100	−100	− 88	− 38	− 38	− 38
α-Gpd	100	100	48	48	48	100	100	66	66	145	117
Pep	100	100	100	100	84	78	78	130	122	182	182
Pgi-1	83	100	140	140	157	140	140	187	187	180	180
Pgi-2	100	100	100	120	100	140	140	240	240	80	80
Got-1	100	100	156	156	156	156	156	100	72	100	200
Got-2	−100	−100	−100	− 73	−100	−100	−100	−100	− 68	−100	− 55
Ipo	−100	−100	−100	−100	−100	−100	−100	−100	−100	− 31	− 31
Alb	100	100	96	100	89	100	100	117	112	112	112
Hb	−100	−100	−100	−100	−100	−100	−100	−100	− 67	−100	−100
Lap	100	100	100	100	100	100	100	100	100	100	100

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 Phyllostomoidea 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 phylogentic 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-

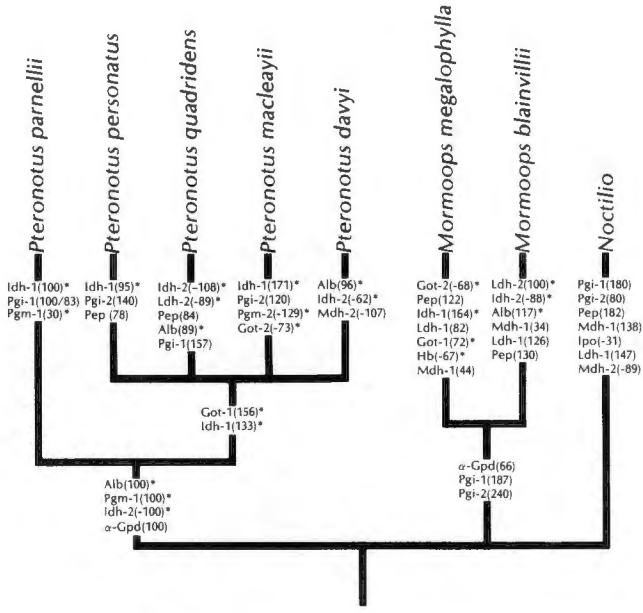

FIG. 1.—Cladogram based on allozymic variants. Allozymes denoted by asterisk were resolved using the outgroup method. See text for identification of abbreviations.

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. parnellii* 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 Phyllostomoidea (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 phyllostomid species *Macrotus waterhousii*. Based on the assumption that the $2n=46$, FN=60 karyotype is primitive for the Phyllostomoidea, the families Noctilionidae and Mormoopidae are linked by five synapomorphies (Robertsonian fusions). Patton and Baker (1978), using the rule of parsimony, indicated that the

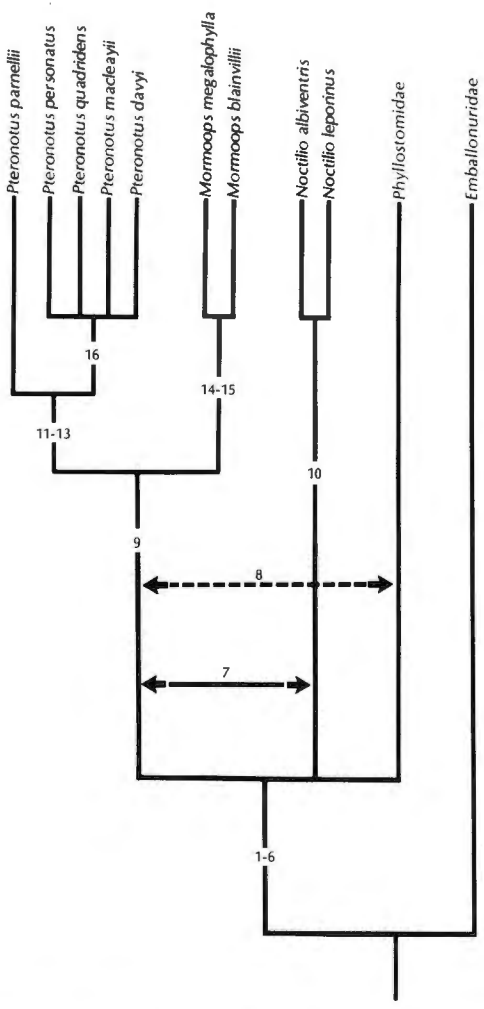

FIG. 2.—Cladogram based on morphological characters examined by Smith (1972): **1**, Premaxillary bones complete and fused to maxillary and palatine bones; **2**, Os penis absent; **3**, Marked sella turcica; **4**, Foramen ovale similarly situated; **5**, Wartlike bumps and ridges on lower lip; **6**, Lanceolate tragus; **7**, Capitulum and trochlea lie in an intermediate position; **8**, Supraglenoid fossa well developed; **9**, Trochanter on proximal end of femur not distinct; **10**, Tragus slender, pinnately-lobed; **11**, Medial process moderate in length; **12**, Capitulum and radius form "tongue and groove"; central part of capitulum larger; **13**, Tragus with secondary fold greatly increased in size and forming major part of structure; **14**, Medial process shortened; **15**, Well-developed tragus fold; **16**, Well-developed secondary tragus fold.

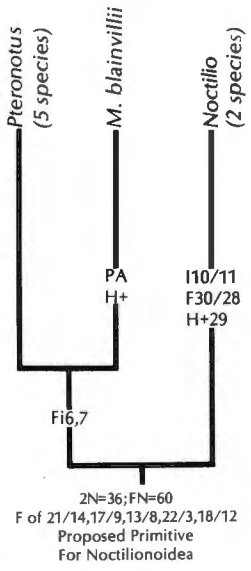

FIG. 3.—Cladogram based on chromosomal data from studies by Patton and Baker (1978), and Baker and Bickham (1980): F=fusion, H+=heterochromatic addition, I=inversion, PA=paracentric inversion.

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 Phyllostomoidea 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 monophylly 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 noctilionid species. The Phyllostomidae sample is a mixed outgroup consisting of* Macrotus, Vampyrum, Glossophaga, Carollia, *and* Desmodus. *The Pteropodidae sample consists of* Syconycteris, Pteropus, Dobsonia, Nyctimene, *and* Paranyctimene.

Taxon	*M.m.*	*P.p.*	*N.l.*	Ph.
Mormoops megalophylla	0	95	146	87
Pteronotus parnellii		0	150	80
Noctilio leporinus			0	135
Phyllostomidae				0
Pteropodidae	140	178	180	172

the antigenic equivalent of 30 to 40 units of albumin immunological distance must have occurred early in phyllostomoid history (Table 2, Fig. 4). Thus, this event has provided an effective phenetic 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 phyllostomoid albumin evolution. This does not, however, affect our cladistic analysis, as the data for phyllostomoid 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 phyllostomid 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 phyllostomid 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 phyllostomids. 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 phyllostomids. Otherwise, the albumin data would not be readily interpretable within the generally agreed upon framework that

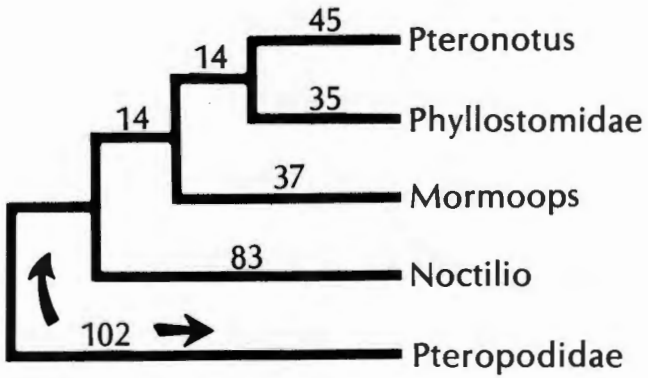

FIG. 4.—Cladogram of the Phyllostomoidea lineages based on the albumin immunological distances of Table 2. The numbers along the lines represent the amount of albumin change allocated to a particular lineage. The Family Pteropodidae is used as an outside reference point to root the tree and apportion the amounts of change among lineages.

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 parnellii* 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 also is quite different from those of other phyllostomoid 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 phyllostomoid 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*-phyllostomid 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 immunologically assessed albumin evolution. However, significant individual 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 individual 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 30 million years), the rate being normal before and after, it is appreciably 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 nonequivalence 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 (Mickevich 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 appropo; 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 chiropterans 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.

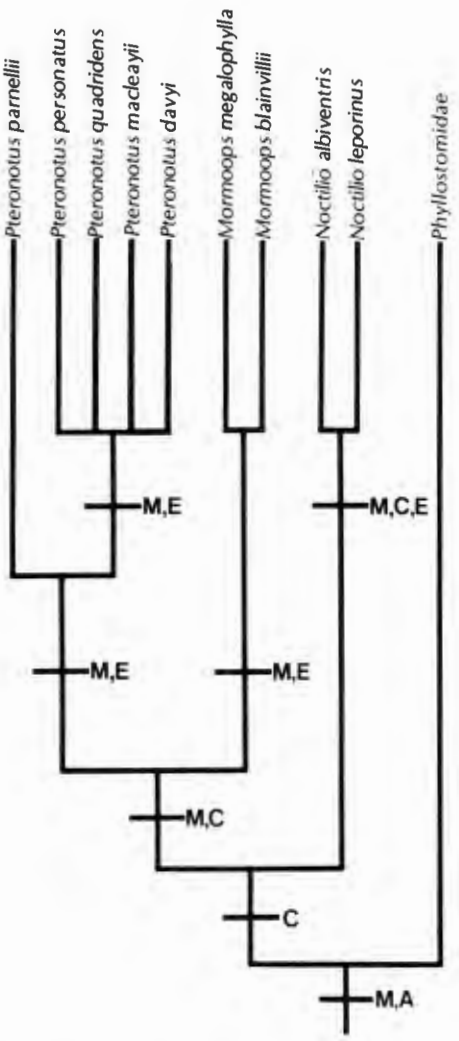

FIG. 5.—Composite cladogram indicating the levels of resolution of each of the character sets used: A=albumin, C=chromosomal, E=electrophoretic, and M=morphological.

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.

Acknowledgments

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