

not ensure that their joint solutions do not interact. This is clearly an undesirable property that is not shared by methods that form groups based only on the spatial relationships of OTUs that are relatively close together. Classifications based on minimum spanning trees (e.g., by using the single-link clustering method) and the UPGMA clustering method are obvious examples of methods that do not have these problems.

The problems discussed above may be part of the reason why a number of empirical studies (e.g., Sokal and Rohlf, 1981; Rohlf et al., 1983) have shown that phylogenetic classifications based on Wagner trees do not have the properties that many workers expected. This is despite the various arguments for its theoretical advantage as a phylogenetic method. The theoretical advantages of classifications based on true phylogenetic trees may not be shared by classifications based on trees from particular statistical estimation procedures.

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## Scientific Method, Opinion, Phylogenetic Reconstruction, and Nectar-feeding Bats: A Response to Griffiths and Warner

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This is a response to two "Points of View" (Griffiths, 1983; Warner, 1983) concerning the systematics of the New World nectar-feeding bats (Phyllostomidae) and criticism of our paper (Haiduk and Baker, 1982) on studies of G-banded chromosomes of this group.

First, we will address Griffiths' paper. We agree with him that there is considerable congruence in the conclusion reached in his morphological study and our study of G-banded chromosomes. It

appears to us that there are two major areas of disagreement, one between the two empirical data sets and the other in systematic philosophy. First, Griffiths concluded that a clade including the genera *Lonchophylla*, *Lionycteris*, and *Platalina* was not closely related to the other nectar feeders, whereas we concluded that this clade fell among the other genera of nectar feeders. We pointed out that our data from G-banded chromosomes were not as definitive as one might hope, and there was the possi-

bility that the *Lonchophylla*-clade represents the first dichotomy in the taxa studied.

The second major disagreement between Griffiths' conclusions and our own is that he concluded that the nectar feeders should be split into four subfamilies (the Glossophaginae, Brachyphyllinae, Phylloonycterinae and Lonchophyllinae). We feel that even if it does prove true that the *Lonchophylla*-clade lies outside what is currently recognized as the Brachyphyllinae and the remainder of the currently recognized Glossophaginae, all of these nectar feeders should still be placed into a single subfamily. If it should prove to be true that Griffiths' *Lonchophylla*-clade did not share a common ancestry with the other nectar feeders examined by him (including the currently recognized Brachyphyllinae), then his proposed new subfamily, the Lonchophyllinae, would be valid. However, with the contradictory nature of available data sets, we do not feel such recognition is justified at this time.

We see no justification for the continued recognition of Brachyphyllinae (composed of *Brachyphylla*, *Erophylla* and *Phylloonycteris*) nor the recognition of subfamilial status for the Brachyphyllinae, Phylloonycterinae and Lonchophyllinae in addition to the Glossophaginae. This conclusion is based on the fact that, while some tentative data exist supporting common ancestry between these taxa, no data support a closer relationship between any of these nectar-feeding taxa and other phyllostomid groups than exists between nectar-feeding taxa. Admittedly, the nectar feeders are a diverse assemblage of taxa, but does that diversity necessarily require the recognition of new subfamilial groupings? We do not see any data justifying such an arrangement at this time.

Also, if the *Lonchophylla*-clade is a valid taxonomic unit, this level of divergence should be reflected in other anatomical and biochemical features. Although *Lonchophylla* was the most divergent of the Glossophaginae studied by microcomplement fixation of albumins, Baker et al. (1981) did

not provide data on the appropriate taxa to tell how divergent *Lonchophylla* was from the other subfamilies of the Phyllostomidae. The use of albumin data in the study of relationships among members of the Phyllostomidae may not provide accurate estimates of divergence because albumin evolution in this group does not appear to proceed in a regular, clock-like fashion (Arnold et al., 1982). Arnold et al. (1982:9) stated "It thus is fair to point out that the 'molecular clock' concept never would have been formulated on the basis of a study of phyllostomid albumin evolution." Data are now needed from other subfamilies in the Phyllostomidae as well as studies to determine if the great distance for *Lonchophylla* is the result of a long period of divergence or irregularities in its rate of evolution.

Warner (1983) has raised some valid criticisms concerning the problems associated with chromosomal characters, especially in taxa with megaevolved karyotypes. Other criticisms raised by Warner, however, are either unsubstantiated or are the result of misinterpretations of the purpose of our original paper. We will begin by addressing criticisms of purpose and then address those dealing with chromosomal data and their analysis.

Warner stated "While Haiduk and Baker (1982) claimed a reanalysis of Griffiths' data indicates that the *most* 'parsimonious' cladogram consistent with the morphological information is identical to their cladogram based on chromosomal data, this is not necessarily true . . ." (Warner 1983:279, italics ours). What we said was "his data are *more* parsimoniously explained by the branching pattern resulting from chromosomal data" (Haiduk and Baker, 1982:262, italics added). The difference between more and most may seem insignificant, but when taken in the context of our paper and Warner's Point of View, there is a substantive difference. Our primary reason for reanalyzing Griffiths' data was to point out the underlying congruence that appeared to exist between morphological and chromosomal data. The critical component of our text which War-

ner apparently overlooked is summarized in the following statement: "The critical point of our reanalysis is that when Griffiths' (1982) data are placed into a cladogram with the same branching sequences resulting from a cladistical analysis of G-banded chromosomes, fewer reversals or convergent events are required to explain his data" (Haiduk and Baker, 1982: 262). We never attempted to produce the *most* parsimonious cladogram but simply to point out that a cladogram for the morphological data that had the same basic branching sequence as one based on chromosomal data was *more* parsimonious than Griffiths' cladogram if strict parsimony is observed in its construction.

Warner (1983) also stated that our study was "clearly a reply to Griffiths' (1982) hypothesis." It was a reply, but only in the context of synthesizing two data sets. Such is a natural consequence of taking all the available data into account when examining a given question and represents nothing more than an attempt to arrive at some congruent representation of reality. The two data sets were generated independently and, because they dealt with the same taxa, it is only natural that a synthesis be done by whichever appeared last. We feel confident that, if our paper had appeared first, Griffiths probably would have addressed our work in a similar manner. As a matter of record, our analysis began in 1979 and the timing of publication of Griffiths' work required extensive re-writing of previous drafts. The commitment required to collect the magnitude of G-band data presented in Haiduk and Baker (1982) and to properly analyze the resulting data makes it obvious that our study had to be designed and conducted prior to the appearance of Griffiths' publication.

Again Warner stated "Although I have doubts about identifying a karyotype as plesiomorphic for the whole family, *since outgroup comparison cannot be performed . . .*" (Warner, 1983:279; italics added). Representatives of the Noctilionidae and Mormoopidae (for which all 10 recognized species have now been G-banded; Sites et

al., 1981) are an appropriate outgroup and such comparisons have been performed (Patton and Baker, 1978). Although Warner might conclude that the analysis and proposed homology is inaccurate (Patton and Baker, 1978; Sites et al., 1981; Baker et al., 1983), to say "outgroup comparisons cannot be performed" is incorrect. Relative to Griffiths' conclusion that our outgroups were too distant, we note that *Macrotus* (subfamily Phyllostominae) is an appropriate outgroup for the glossophagines and such outgroup comparisons have been made (Baker and Bass, 1979). Additionally, comparisons of *Artibeus*, *Sturnira*, and *Uroderma* with the karyotype proposed as primitive for the glossophagines (Baker et al., 1982) revealed that the proposed primitive for the Stenodermatinae (Baker et al., 1979) shares few if any synapomorphies with the proposed primitive for the Glossophaginae.

None of the studies (Patton and Baker, 1978; Baker and Bickham, 1980; Baker et al., 1981; Sites et al., 1981) on cladistical analyses of G-banded chromosomes of the Phyllostomidae have ever concluded that outgroup comparisons cannot be made. It is true that outgroup comparisons for the superfamily, Phyllostomoidea, have not been performed. However, it is clear that only five chromosomal rearrangements distinguish the karyotype of *Macrotus waterhousii* (which is identical to that proposed as primitive for the family) from that found in two species of *Noctilio* and most mormoopids (Sites et al., 1981). Most of the proposed primitive linkage groups are found in representatives of the Phyllostominae, Glossophaginae, Carrollinae, and Stenodermatinae. These abundant data strongly indicate that the primitive karyotype for the family is similar to that found in *Macrotus waterhousii* (less probably like that found in *Noctilio* and mormoopids) and that the primitive for the Glossophaginae is like that found in *Glossophaga* and *Brachyphylla*. Although Warner (1983) may be of the opinion that the study of G-bands is not valid for systematic studies, there is a wealth of data (specifically on the phyllostomoid bats and on other mammals and

other vertebrates in general) that we find difficult to dismiss. Workers from our and other laboratories have concluded that it is possible to recognize G-band homology between families (Dutrillaux, 1979; de Grouchy et al., 1978; Creau-Goldberg, 1981; Bickham, 1981; Yunis and Prakash, 1982).

As justification for rejecting data generated from analysis of G-banded chromosomes, Warner (1983) indicated that he had trouble identifying segments that we have stated are homologous between taxa. In reality, it is relatively unimportant whether someone is able to identify similar segments from published figures. What is important concerning the process of assigning G-band homology can be reduced to two primary groups of questions. First, are reproducible results possible? Do independent workers come to identical conclusions concerning which segments are homologous? Second, do the G-banding patterns accurately document genetic homology of chromosomal segments?

The first question is easily tested. By having several different researchers examine the same spreads and identifying them to a standard, one can provide a direct measure of how reproducible this technique is. We did this a number of years ago at Texas Tech and came to the conclusion that, if the researchers were well experienced in comparing G-banding patterns, the results were reproducible. For the best spreads, over 90% of the arms were identified as the same by different workers. However, in all examples where there were small chromosomes, some of these elements were not consistently identified by independent workers as homologous. These observations formed the basis for the statement in Baker and Bickham (1980: 240), "Some comment is merited on the reliability of the above methods of determining the amount of rearrangements in the phylogeny of a species. We are sure that, within the families Phyllostomatidae and Vespertilionidae, there are some errors in identifying homologous G-band segments of chromosomes between divergent taxa; however, we think that the error level is below 10 percent." We obviously agree

with Warner's (1983) conclusion that determining homology between segments can be difficult and workers from this laboratory have so stated (Baker and Bickham, 1980). However, we also are of the opinion that, with proper careful examination of several to many spreads, these types of studies are reproducible.

Concerning Warner's (1983) specific criticisms on the assignment of chromosomal homology several points can be made. First, arm E of many of the taxa examined is clearly different than 23-24i of *Glossophaga* in several respects. Relative to the remainder of the genome, arm E is roughly twice the size of the 23-24i element in *Glossophaga* but not as large as the entire 21-24i/21 element found in *Glossophaga*: Based on the banding sequences, it appears that the most probable origin of arm E is from the 27/22 chromosome of *Glossophaga* by an inversion. This conclusion is based on the fact that the 27/22 is of appropriate size and also the two terminal G-positive bands in arm E match two bands characteristic of arm 27. An inversion in this chromosome to produce an acrocentric chromosome would also produce a pattern of lighter, subtle banding that corresponds to the pattern seen in arm E.

Warner also was unsure of our ability to distinguish between the 13/2, 13/18 and 2/28 chromosomal combinations. Arms 2 and 18 are easily distinguished on the basis of banding patterns. Arm 2 has a distinct arrangement that can be summarized as follows: a large G-negative band proximal to the centromeric region, followed by a fairly thick, intensely staining G-negative band, then a moderately sized G-negative region, another G-positive band which is narrow and moderately staining, another fairly broad G-negative band, a set of two closely placed G-positive bands that are separated by a narrow G-negative band, and finally a terminal G-negative telomeric band. Arm 18 is similar in overall appearance but a close analysis reveals many differences in the banding pattern. The only real similarity between the two is that both have a fairly thick, densely staining G-positive band. The position of

this band is different as are the other bands found in arm 18; between the centromere and the thick G-positive band (which is positioned more medially in arm 18 than it is in arm 2) is a G-negative region with at least 3 G-positive bands included. Distal to the thick, G-positive band is an alternating pattern of G-negative and G-positive bands (3 and 2, respectively) none of which are as broad or intensely stained as in chromosome 2. These banding characteristics of arms 2 and 18, respectively, are observable in taxa ranging from mormonopids and noctilionids to other phyllostomids and can be easily discriminated. When the chromosomal element in the derived glossophagines was examined in side-by-side comparisons we determined that the distal one half of the arm in question corresponded exactly in banding pattern to chromosome arm 2.

The possible 2/28 fusion proposed by Warner to account for the chromosome we identified as a 13/2 can be ruled out on the basis of size considerations and differences in banding pattern. Linkage groups 13 and 28 are similar in appearance because both possess one medially positioned G-positive band, but the 28 is half the size of 13. Additionally, between the dark G-positive band and the centromere is a relatively broad G-negative band in 28, but this region in 13 stains darker and includes several fine G-positive bands. There are also subtle bands in the region distal to the intense G-positive band of arm 13 (a region not even present in 28) that match a region in the proposed 13/2 fusion just above (proximal to) the "centromeric" region of arm 2. Thus, if side-by-side comparisons are made, it is found that the chromosomal element in question is essentially a perfect match to the proposed tandem fusion of 13 and 2.

Warner also suggested that the inversion in the *Lonchophylla* 13/2 would make a bad situation even worse in terms of our ability to recognize homologies. It is true that rearrangements can potentially make homologies difficult to recognize, but in this specific case two factors eliminate this problem. First, as outlined above, we have

no difficulty in recognizing the 13/2 combination. Secondly, the inversion involved in the *Lonchophylla* chromosome involves only a very small region, proximal to the centromere, such that the centromere position has been shifted but the vast majority of the banding sequence of this arm has been undisturbed. Therefore, we feel that there is a very high probability that the identification of the 13/2 is accurate, even in *Lonchophylla* where it has undergone a pericentric inversion.

The second question regarding the correlation between G-band patterns and genetic homology of chromosomal segments is an important one to address. Several studies provide evidence that there is an association between G-band patterns and genetic homology (Francke and Taggart, 1980; Stubblefield, 1980; Creau-Goldberg et al., 1981; Ma et al., 1982). There appear to be certain linkage groups, such as those associated with the X chromosome, that are conserved in many diverse organisms (Stock and Hsu, 1973). Additionally, linkage groups have been found to be conserved in organisms as divergent as *Mus musculus* and man (Lalley et al., 1978). Franke and Taggart (1980) mapped specific genes to the X chromosome in both humans and *Mus*, but determined that the order of these genes was different. The different order of genes was apparently produced by an inversion that corresponded to an inverted segment as determined by G-band analysis.

Another point not considered by Warner (1983) is that studies involving other sorts of data, such as electrophoretic, morphological, or microcomplement fixation, do not present raw data that allow detailed reexaminations of a given study from the published account. The best one can hope for is representative figures which accompany processed data. Our figures were presented as representative of the kinds of data being analyzed. Warner's inability to determine homology from them is not surprising in light of the fact that before homologous status is assigned, chromosomal segments from many cells are examined in side-by-side comparisons.

Electrophoretic studies involve a comparable situation in that, before conclusions are drawn concerning genetic similarity or difference at each locus, numerous side-by-side comparisons of the various allelic forms must be completed. However, if the authors of an electrophoretic study were required to document all of their conclusions for a given locus on a photograph of a gel, the result would be no more impressive than our single photograph of G-banded chromosomes. We are not aware of any systematic study where the raw data are presented so that other workers can completely reanalyze the study without examination of the data sheets, gels, microslides, etc., or by the study of additional specimens.

The problems indicated by Warner for chromosomal data are not unique to chromosomal data sets. Within the phyllostomid bats, the generation of electrophoretic data is difficult and researchers can draw inaccurate conclusions as exemplified by Straney et al. (1979), where these authors concluded that *Desmodus* and *Glossophaga* are closely related as documented by a Nei's (1972) genetic distance of 0.35 (a conclusion that was retracted by a note added in galley because further research documented that these two genera shared very few alleles). Nei's genetic distance value published by Honeycutt et al. (1981) for these two genera is 1.23.

The point that we wish to make from the above is that different types of data sets have different problems and in most cases there must be the development of a certain amount of research skill that goes beyond the level of other workers who have no experience in a specific area. Also, we note that the problems associated with identifying homology and directionality in transformation series in chromosomal data sets, which Warner (1983) indicated are reasons to reject our systematic conclusion, are not unique to chromosomal data. These problems continually plague all attempts at phylogenetic reconstruction, no matter what type of data is employed.

Warner (1983:282) stated that "It ap-

pears that at the current level of technical resolution chromosomal banding patterns cannot provide sufficient unambiguous information to assess phylogenetic relationships within groups, such as the 'glossophagines,' in which there has been extensive repatterning of the karyotypes . . . ." However, there are examples where G-banded chromosomes are valuable in showing relationships in forms with a highly rearranged karyotype. An example is the relationship of *Hylonycteris* to *Choeroniscus*, *Choeronycteris* and *Musonycteris*. Phillips (1971) and Gardner (1977) both concluded that *Hylonycteris* was not closely related to these three genera; however, seven chromosomal synapomorphies identify a clade (see fig. 8 of Haiduk and Baker, 1982) containing the four genera and five other synapomorphies identify *Hylonycteris* as sharing a common ancestor with *Choeronycteris* and *Musonycteris* after separating from the *Choeroniscus* lineage. The highly reorganized karyotypes, such as those in the *Choeroniscus* group, are hard to derive from a primitive condition such as in *Glossophaga* because the degree of resolution is inadequate to identify all primitive segments and the types and sequences of rearrangements that have occurred. However, within the *Choeroniscus* group, homology can be determined with a high level of confidence and, although the statement "Plus seven totally rearranged arms" in our cladogram (Haiduk and Baker, 1982:261, fig. 8) may sound vague and uncertain, what it means is that seven major arms as shown in fig. 7 are synapomorphies for this group. The number and types of rearrangement events are uncertain, but the homology of the resulting chromosome arms within this group is as probable as homologies proposed for other characters used in bat systematics. The complexity and number of chromosomal synapomorphies (Baker et al., 1983) certainly suggest that the proper relationship for these taxa has been defined. On the basis of morphological data, Griffiths associated these four genera but he concluded that in some cases "the characters

of the hyoid and lingual regions are insufficient to distinguish between them, and I must rely on dental and karyotypic observations" (Griffiths, 1982:40). The fact that G-band chromosomal data provide synapomorphies, in examples as shown above, documents the fallacy of Warner's (1983) logic. Although opinions such as those expressed by Warner (1983) can be important because they may inspire someone to design a critical study, one should not lose sight of the fact that scientific conclusions must ultimately be based on empirical data.

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