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## On the Monophyly of Bats

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Did powered flight evolve once or twice in mammals? A heated debate has recently developed concerning the phylogenetic relationships of Microchiroptera, Megachiroptera, Primates, and other placental mammals. Two competing hypotheses (Fig. 1) have been proposed to explain the relationships among these groups and the nature of the most recent common ancestor of all organisms we consider to be "bats." In the classical hypothesis (e.g., Wible and Novacek, 1988), Chiroptera forms a monophyletic group relative to all other mammals, and the most recent common ancestor

of Megachiroptera and Microchiroptera would have been easily recognized as a bat. A corollary of this hypothesis is that powered flight evolved only once in mammals, somewhere along the lineage leading to a monophyletic Chiroptera. An alternative hypothesis advanced by Pettigrew and others (e.g., Smith and Madkour, 1980; Pettigrew, 1986; Pettigrew et al., 1989) proposes that flight, and the remarkably similar flight mechanisms seen in Microchiroptera and Megachiroptera, evolved independently in each of these two lineages. Megachiroptera is interpreted as be-

ing most closely related to primates and dermopterans (gliding lemurs), the sister clade of Microchiroptera being unresolved. Under this scheme, the last ancestor common to *all* bats (Megachiroptera + Microchiroptera) was some sort of primitive eutherian, a quadrupedal animal that definitely did not have wings.

Accurate (or at least robust) hypotheses of phylogeny are important for many reasons, not the least of which is that they provide a basis for understanding evolutionary processes and the tempo and mode of evolution. Because the controversy over bat relationships concerns the history of the primate clade—a group of special interest to zoologists, paleontologists, and anthropologists alike—the outcome will be particularly significant. Good phylogenetic studies depend upon making appropriate morphological and (if available) molecular comparisons, and knowledge of the branching sequence of outgroups can be crucial. Is the sister clade of primates a terrestrial, arboreal, or volant group? Did wings evolve more than once in mammals? Our perception of mammalian evolution, and our ability to resolve the higher-level relationships among taxa within each of the groups in question, depends upon the outcome of this controversy.

New arguments draw passionate interest when they suggest the implausible. How could groups so apparently alike as megachiropteran and microchiropteran bats be unrelated? Yet apparently strange hypotheses of relationships among mammals are not uncommon—close relationships between hyraxes and elephants, and between whales and ungulates, are just two examples of hypotheses that have received support from many recent workers (e.g., Novacek and Wyss, 1986; McKenna, 1987; Gingerich et al., 1990; Novacek, 1990). Despite the controversial nature of debates over higher-level mammalian phylogeny, one should not be distracted from basic issues in systematic biology. The monophyly of bats cannot be accepted or rejected on the basis of pure intuition. This problem is simply another, albeit very interesting, example of apparent conflicts in

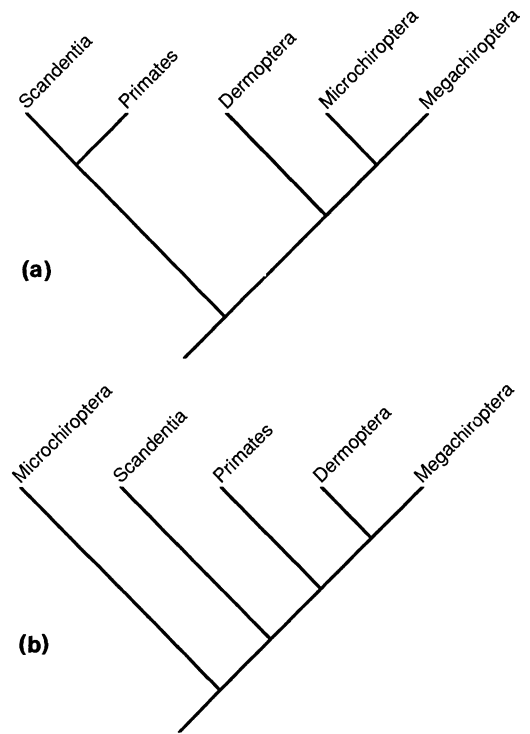


FIGURE 1. Two competing hypotheses concerning the phylogenetic relationships of microchiropteran bats, megachiropteran bats, primates, dermopterans (gliding lemurs), and scandentians (tree shrews). (a) "Classical" hypothesis, supported by Wible and Novacek (1988) and others. (b) Alternative hypothesis, supported by Pettigrew et al. (1989) and others.

character data and the different perspectives that are brought to bear on resolving such conflicts.

Pettigrew and his colleagues (Pettigrew, 1986; Pettigrew and Cooper, 1986; Pettigrew et al., 1989) have energetically promoted the argument that megachiropterans share important derived features in neural structure with primates and dermopterans that point to a close kinship to these groups and rule against affinities with microchiropterans. This view corresponds with earlier support for this arrangement based on studies of penial morphology (Smith and Madkour, 1980). The outlay of comparative work recently provided by the advocates of bat nonmonophyly is impressive (Pettigrew et al., 1989). Nonetheless, we find serious shortcomings in the Pet-

TABLE 1. Unique features of the postcranial musculoskeletal system shared by Microchiroptera and Megachiroptera. Presence of these derived features in bats (but not in any other placental mammals) suggests that Chiroptera is monophyletic.

1. Occipitopollicalis muscle along leading edge of propatagium.
2. Reduced supraspinous fossa and enlarged infraspinous fossa on scapula.
3. Strongly arched acromion process on scapula.
4. Distal end of humerus without supratrochlear depression and supinator ridge.
5. Markedly reduced olecranon process on ulna.
6. Digits 2-5 of forelimb greatly elongated.
7. Manus rotated 90°.
8. Proximal metacarpals deeply grooved, strongly imbricated.
9. Claws restricted to digit I or I and II on forelimb.
10. Extreme lateral flaring of pubes.
11. Dorsal ischia meet above vertebral axis.
12. Dorsolateral tilting of sites of origin for gluteal muscles.
13. Iliosacral fusion involving last lumbar vertebra.
14. Hindlimbs rotated 90° outward so knee is directed laterally.
15. Head of femur tilted and nearly aligned with long axis of the shaft.
16. Calcaneal astragalar facet on calcaneum concave or trough-shaped (not convex).
17. Loss of medial and lateral guiding ridges on trochlea of astragalus.
18. Presence of calcar and depressor osseus styloformis muscle.

tigrew et al. (1989) assessment of neural structures, in their emphasis on differences rather than derived similarities in wing structure, in their lack of alternatives for implicit weighting of the conflicting characters, and in the scope of their comparisons and outgroup assumptions. We also disagree with aspects of their interpretations of data previously published in support of bat monophyly. If there is a strong case to be made for diphyly of bats, it is not foreshadowed by the evidence at hand. Our position is that the highly specialized wing and associated structures, plus evidence from several other data sets (e.g., skull morphology, cranial vasculature, axial skeleton, hindlimb morphology, fetal membranes), favor a hypothesis of chiropteran monophyly.

#### WING STRUCTURE AND FLIGHT

Any analysis of bat relationships must take into account one essential observation: among mammals, powered flight (and numerous correlative structures of the wing) is found only in Megachiroptera and Microchiroptera. Despite attempts to downplay the significance of this fact (e.g., Smith, 1977; Pettigrew et al., 1989), it is difficult to think of any mammalian order that can be diagnosed by such a richly en-

dowed character system (Table 1). One can easily enumerate many unique specializations in the musculoskeletal system associated with bat wings (e.g., Vaughn, 1970a, 1970b; Novacek, 1982; Wible and Novacek, 1988), but how these features are incorporated into a phylogenetic analysis is another matter. Whether wing structure is scored as one heavily weighted character or many lightly weighted characters does not detract from the possibility that the wing is a synapomorphy of bats. Its status must be judged against the weight of contradictory evidence from other character systems.

In making this point, we reject any claims that there are major *intrinsic* difficulties with the use of wing structure and powered flight as evidence for bat monophyly. Pettigrew et al. (1989) suggested that the neural characters associating megachiropterans with primates are somehow superior to similarities in flight and wing structure in terms of their ability to resolve phylogenetic relationships. They noted that wings and powered, flapping flight evolved independently in teleosts, pterosaurs, birds, and mammals, and that gliding flight evolved numerous times in vertebrates. Hence, Pettigrew et al. (1989:520) concluded that

One may therefore be on safer ground in proposing that flight has evolved in parallel in a branch of the primates relative to microbats, rather than proposing that flight in megabats and microbats is monophyletic and that megabats have independently evolved all the functionally obscure details of neural connections found in primates. We say 'functionally obscure' to emphasize the fact that there is currently little understanding of the functional significance of most of the neural features used in our analysis. . . . This stands in contrast to the well-recognized functional constraints operating on the wing.

This statement betrays an evaluation of characters that runs somewhat ahead of the evidence. The number of times a feature appears in some groups does not necessarily predict its tendency to appear in others. Prevalence of limblessness among amphibian and lepidosaurian burrowers is not echoed among mammalian burrowers, all of which have functional limbs. Pterosaurs and birds have wings, but why does this offer compelling evidence that wings evolved more than once within mammals? We are not led to believe that flight evolved several times within vertebrates simply because flight was also attained in insects; instead, close comparisons of different vertebrate taxa provide the telling evidence. The independent evolution of flight in vertebrates seems reasonable because we believe that pterosaurs, birds, and bats each show fundamentally distinctive forelimbs that can be derived from patterns common to their closest relatives. The diversity of possible solutions to powered flight in vertebrates is illustrated by the fact that the wings of pterosaurs differ distinctly from those of bats: only one digit supports the wing of pterosaurs, whereas four digits support the bat wing. So why are all bat wings so similar, when wings can obviously be designed in many different ways? Pettigrew et al. (1989:523) argued that

. . . the single digit extension used by pterosaurs may not have been available as an option to mammals because this option also required the presence of actinofibrillae that mammals lack.

But this merely explains why bat wings are different from those of pterosaurs. It does not logically follow that the wings of megachiropterans and microchiropterans

must have evolved convergently as a reflection of functional constraints (Pettigrew et al., 1989:521-522). A membranous wing lacking actinofibrillae might be supported effectively by three elongate digits rather than the four seen in megachiropterans and microchiropterans—there are many possibilities. Scenarios such as these cannot be tested and thus can contribute little to resolution of the questions at hand.

Implicit in the discussions presented by Pettigrew et al. (1989) is the premise that features of obvious functional and adaptive significance (like the chiropteran wing) are subject to higher levels of homoplasy than other characters. Multitudinous features, including the amnion of amniotes, mammary glands of mammals, and conserved regions of ribosomal DNA, would be potentially vulnerable to this argument. We hardly need belabor an objection to this premise; suffice to say that the consistent use of this "adaptive criterion" to dispense with phylogenetic evidence may lead to eventual elimination of *all* data! Why must phylogenetically compelling characters be devoid of function? In fact, discovery of function for structures can enrich the case for monophyly (e.g., the feeding apparatus of cichlid fishes discussed by Lauder [1981]). It thus seems curious to argue that the "functionally obscure" neurological connections (Pettigrew et al., 1989: 520) are somehow superior to wing structure as evidence for bat relationships. Furthermore, it seems unlikely that the neural characters cited by Pettigrew et al. (1989) are actually without function; a more reasonable assessment is that we simply do not yet understand the functions of these features. For example, various improvements in binocular vision, eye-hand coordination, depth perception, detailed object vision, and motion detection have been suggested as explanations for some of the derived features of the optic tract (Kaas, 1986; Sanderson, 1986). Inability of current techniques to pinpoint specific functions of various nuclei and cell layers does not preclude future understanding of the functions of these structures.

Another tactic used to minimize the case

for homology of the wings in the two bat suborders is to emphasize the obvious differences in wing structure. In this vein, Pettigrew et al. (1989) provided an exacting and lengthy discussion of the stark contrast in the metacarpophalangeal index (M/P index; the ratio of the metacarpal length to the length of the first phalanx in the third and fourth digits) between megachiropterans and microchiropterans. There is little reason to doubt, from this analysis, that this index does indeed separate the bat suborders. However, these data do not substantiate the authors' assertion that the index "... however it be interpreted, objectively denies the claimed high degree of similarity between the two kinds of wing" (Pettigrew et al., 1989:524). In their enthusiasm, these authors failed to explain why all the unique features of the musculoskeletal system held in common between Megachiroptera and Microchiroptera (Table 1) are denied by a comparison of this ratio. Moreover, it is unclear to us why this single index should have any more valency than any one of the musculoskeletal features, or, for that matter, any other measurement or ratio. Because neither metacarpal nor phalanx length remains constant relative to body size among placental mammals, similar M/P index values do not necessarily reflect similar patterns of hand structure (e.g., a low ratio can be produced by either relative lengthening of phalanges or relative shortening of metacarpals). It seems unlikely that the M/P index reflects any useful information about homology, particularly when volant, arboreal, scansorial, and cursorial organisms with structures ranging from wings to digitigrade hands are compared (e.g., Pettigrew et al., 1989: their Table 4 and Fig. 15). Pettigrew et al. (1989) have selected an interesting morphometric variable (out of a universe of traits) that says something about the differences between megachiropterans and microchiropterans, but says nothing about their affinities to each other or to other mammals.

This emphasis on function and phenetic difference was taken to the extreme in the Pettigrew et al. (1989:542) assessment of

the musculoskeletal features of bat wings. They cited the characters listed as bat synapomorphies by Novacek (1980) as problematic merely because each character might be independently derived if flight evolved twice in mammals. Thus the occipitopollicalis muscle is eliminated (even though it is unique to bats) because this muscle functions to maintain the leading edge of the wing, an essential function for effective flight. The rotation of the manus and hindlimb, and various details of the forelimb are "all more or less to be expected, if not obligatory, in a hand wing" (Pettigrew et al., 1989:543). What they seem to regard as strong evidence for homoplasy are differences found between these structures, in spite of their similar functional roles. The scapula, despite the distinctive enlargement of the infraspinous fossa, is rendered a dubious synapomorphy because this fossa has more facets in microchiropterans than in megachiropterans. The authors are speaking a different language here—one that mixes the world of differences with a world of underlying (homologous) similarities. We see little hope for resolution when such a dialect is adopted.

#### DERIVED FEATURES NOT ASSOCIATED WITH FLIGHT

Because bats, like other organisms, are mosaics of traits, a consideration of their affinities should not be confined to a single functional system such as the wing. Accordingly, Wible and Novacek (1988) described several additional specializations shared by Megachiroptera and Microchiroptera (Table 2). These were rejected as compelling evidence by Pettigrew et al. (1989) largely because they occur in a few other mammals, or because the taxa drawn into the comparisons were inappropriate. It is acknowledged that at least one of these features, the development of the premaxilla (Table 2, character 1), has a problematic distribution susceptible to alternative interpretations. We find, however, that the Pettigrew et al. (1989) analysis failed to account for the explanations of the other characters as they were originally de-

TABLE 2. Derived features of the skull, cranial vascular system, fetal membranes, and nervous system shared by Microchiroptera and Megachiroptera (from Wible and Novacek, 1988: their Table 3). These features are absent in Primates, Dermoptera, and Scandentia, and were interpreted as synapomorphies of Chiroptera by Wible and Novacek (1988).

1. Premaxilla greatly reduced.
2. Jugal greatly reduced.
3. Tegmen tympani tapers to a slender process that projects ventrally into the middle-ear cavity medial to the epitympanic recess.
4. Two entotympanic elements in the floor of the middle-ear cavity: a large caudal element and a small rostral element grooved by (or forming a canal around) the internal carotid artery.
5. Ramus inferior of the stapedia artery passes through the cranial cavity dorsal to the tegmen tympani.
6. Ramus infraorbitalis of the stapedia artery passes through the cranial cavity dorsal to the alisphenoid.
7. Preplacenta broad and horseshoe-shaped, with definitive placenta more localized.
8. Prominent interstitial membrane in chorioallantoic placenta.
9. Cortical somatosensory representation of forelimb reverse of that in other mammals.

scribed by Wible and Novacek (1988). Contra Pettigrew et al. (1989), Wible and Novacek (1988) went to some effort to provide an ontogenetic argument for why the derived megachiropteran tegmen tympani is much more similar in structure to that of microchiropterans than that of primates or any other placental mammals. Pettigrew et al. (1989) additionally judged the entotympanic, vascular, and fetal membrane traits as problematic because similar patterns occur in some members of some outgroups, but they did not give due consideration to Wible and Novacek's (1988) argument that such patterns are not strictly homologous in bats and other mammalian groups.

One interesting neural character cited by Wible and Novacek (1988) as a bat synapomorphy is reversal of the somatosensory representation of the forelimb. Somatosensory input from various parts of the body is received by specific areas of the neocortex in mammals, and maps of these areas reveal a similar orientation of forelimb representation in marsupials, rodents, carnivorans, scandentians, and primates (Johnson, 1980; Kaas, 1980). Somatotopic maps have been compiled for only three bats. In one microchiropteran (*Macroderma gigas*) and one megachiropteran (*Pteropus poliocephalus*), somatosensory forelimb representations are the reverse of that of the body, which maintains the same relative position as seen in somatotopic maps of other mammals (Calford et al., 1985; Wise et al., 1986). One

microchiropteran (*Antrozous pallidus*) has been reported to lack this reversal of the forelimb representation (J. M. Zook and B. C. Fowler [reported in Pettigrew et al., 1989: 519]), but data supporting this claim have not yet been published. Because the pattern seen in *Macroderma* and *Pteropus* is unique within mammals, this pattern can be interpreted as either (a) a feature that evolved independently in these two taxa or (b) a synapomorphy of Chiroptera that may have been later reversed within Microchiroptera. The latter argument may be strengthened by the observation that *Antrozous pallidus* is a terrestrial insect gleaner capable of agile terrestrial locomotion, during which it uses its forelimbs in a posture unlike that used for flight (Hill and Smith, 1984; Pettigrew et al., 1989). As this behavior and posture are presumably derived within vespertilionid microchiropterans (Hill and Smith, 1984), concomitant evolution of a secondarily derived somatotopic representation of the forelimb can be hypothesized. Pettigrew et al. (1989) were correct in noting that the distribution of this character has not been adequately sampled, but existence of a possible synapomorphy of bats in the nervous system should not be overlooked.

The claim that the characters in Table 2 provide dubious evidence because they have not been sampled adequately or are not unique to bats seems oddly severe for a study that places heavy emphasis on features that are subject to the same criticisms.

Those neural traits recruited to support megachiropteran–primate–dermopteran affinities are *not* devoid of patterns that suggest homoplasy, and the taxonomic sampling for these traits was clearly not adequate in the Pettigrew et al. (1989) study (see below).

#### ANALYSIS OF THE VISUAL NEURAL SYSTEM

Numerous studies in the last decade have suggested that features of the mammalian nervous system may provide information useful for phylogenetic analyses (e.g., Kaas et al., 1978; Switzer et al., 1980; Johnson et al., 1982a, 1982b; Kirsch, 1983; Kirsch and Johnson, 1983; Kirsch et al., 1983; Johnson, 1986; Pettigrew, 1986; Pettigrew and Cooper, 1986; Sanderson, 1986; Kaas and Huerta, 1988; Pettigrew et al., 1989). Pettigrew and his associates (Pettigrew, 1986; Pettigrew and Cooper, 1986; Pettigrew et al., 1989) have recently argued that pathways related to the visual system seem particularly informative, an assessment that appears justified based on their work. As with any other data, however, neural characters must be appropriately sampled and analyzed before they can contribute to our understanding of mammalian phylogeny. Our examination of the Pettigrew et al. (1989) analysis of neural features reveals some critical shortcomings that bear on the issue of bat monophyly.

Pettigrew et al. (1989) used 24 characters from the nervous system in their cladistic analysis of chiropteran and primate relationships. Many of these features have interesting distributions suggesting preservation of important phylogenetic information, but the methods used to score these characters for analysis are problematic. For example, 12 of the characters considered by Pettigrew et al. (1989) come from the dorsal lateral geniculate nucleus (dLGN), a nucleus in the thalamus that relays information from the retina to the visual cortex of the brain. Laminar differentiation of the dLGN is considered to be a derived condition, so taxa lacking such differentiation are scored as possessing the primitive condition of this character. Of the remaining dLGN characters, eight depend upon

the presence of laminar differentiation; an organism with no laminae in the dLGN cannot, by definition, possess the derived conditions of any of these characters. However, organisms with laminar differentiation can also lack the derived conditions. In scoring these sorts of characters for analysis, Pettigrew et al. (1989) interpreted all conditions that are *not* derived to be equivalent, and scored this category as primitive. In doing so, these authors failed to distinguish between clearly different conditions. For example, three different conditions were scored as a single primitive character state in Pettigrew et al.'s (1989) character #6 (position of the magnocellular layers in the dLGN). Separation of the magnocellular layers from the optic tract by intervening cell layers, a condition seen only in the tree shrew *Tupaia*, was effectively equated with absence of a magnocellular layer in a laminated dLGN (seen in gliding squirrels) and absence of all layers (a consequence of lack of laminar differentiation; seen in microchiropterans and tree sloths). All three conditions were scored as a primitive state described as "magnocellular layers not adjacent to the optic tract" (Pettigrew et al., 1989:512).

This method of scoring characters for analysis obscures the data actually collected by Pettigrew et al. (1989), and has serious implications for the outcome of their analysis. For example, the scoring scheme used by Pettigrew et al. (1989:512) requires eight reversals in characters related to dLGN lamina if Microchiroptera is placed as the sister group of Megachiroptera. In this case, it is not clear why one reversal—simple loss of laminar structure in the dLGN of microchiropterans—cannot explain the observed differences between Microchiroptera and Megachiroptera. Methods of scoring characters clearly play a crucial role in computer-assisted phylogenetic analysis; available algorithms analyze the codes entered into the computer, not the actual data. In the case of Pettigrew et al. (1989), rescored the characters probably would not change the resulting phylogeny, but would significantly affect accompanying hypotheses of character

evolution and the level of perceived support for various nodes in the cladogram.

Another serious weakness of the study presented by Pettigrew et al. (1989) concerns taxonomic sampling. In a cladistic analysis, choice of taxa can significantly affect the resulting phylogeny in several ways. Proper use of outgroups (at least two) is crucial for correct assessment of character polarities (Maddison et al., 1984). Similarly, insufficient sampling of within-group variation can lead to incorrect assumptions about homology of derived conditions among various taxa, prejudicing resulting phylogenies. Pettigrew et al. (1989) presented a phylogenetic analysis that was clearly biased by the choice of the taxa that were included. Although many additional taxa were discussed in the text, Pettigrew et al. (1989) limited their formal cladistic analysis to 14 taxa: 5 primates, 2 megachiropterans, 2 microchiropterans, 1 dermopteran (the gliding lemur, *Cynocephalus*), 1 tree shrew (*Tupaia*), 1 rodent (a gliding squirrel, *Petaurista*), 1 elephant shrew, and 1 edentate (a tree sloth, *Bradypus*). This set of taxa provides an adequate basis for a preliminary analysis of phylogeny based on neural characters, but close inspection of the results indicates that more taxa *must* be considered to test properly the hypothesis of bat monophyly.

In order to test the monophyly of Chiroptera and the relationship of Megachiroptera to Primates, at least two outgroups must be found that clearly lie outside the smallest monophyletic group that includes all bats and primates (whatever the composition of that group). Recent phylogenies of Mammalia (e.g., McKenna, 1975; Novacek and Wyss, 1986; Novacek et al., 1988) suggest that rodents, elephant shrews, and edentates all fall outside the smallest monophyletic group that includes primates and bats. On this basis, these taxa seem to represent adequate outgroups for testing the hypothesis of chiropteran monophyly. However, the analysis of Pettigrew et al. (1989) resulted in a cladogram in which Microchiroptera is the most distal branch; the other taxa considered (tree sloth, elephant shrew, rodent, and tree

shrew) are shown to be more closely related to Megachiroptera than is Microchiroptera. This arrangement suggests that Chiroptera is diphyletic, but does not support this interpretation unequivocally because no effective outgroups (taxa that lie outside the group Megachiroptera + Microchiroptera) are present. Absence of outgroups means that characters cannot be polarized adequately and that the resulting phylogeny must be considered suspect. Inclusion of outgroups (perhaps monotremes and marsupials) in a formal reanalysis is crucial before the results of Pettigrew et al. (1989) can be interpreted as evidence that bats are not monophyletic.

Bias can also be introduced into phylogenetic analysis if within-group variation is not adequately sampled. In the analysis presented by Pettigrew et al. (1989), the taxonomic sampling seems to be appropriate for most groups. Among the primates, bats, gliding lemurs, elephant shrews, and edentates, the level of sampling seems adequate because the genera chosen for analysis appear to exhibit the full range of variation known within the orders they belong to, at least with regard to the visual neural system (Kaas et al., 1978; Sanderson, 1986; Pettigrew et al., 1989). The tree shrew and the rodent, however, represent genera known to possess among the most highly differentiated visual systems within their respective orders (Sanderson, 1986; Pettigrew et al., 1989). *Tupaia*, for example, has five or six well-defined cell layers in the dLGN, but its close relative *Ptilocercus* (pen-tailed tree shrew) is known to have a much simpler dLGN with no cellular laminae (Simmons, 1979). All squirrels so far examined have a strongly laminated dLGN, whereas other rodents do not, and gliding squirrels exhibit a pattern of retinal inputs unique within Sciuridae (Sanderson, 1986). Given the characters considered by Pettigrew et al. (1989), it seems likely that inclusion of a less visually specialized rodent (e.g., *Mus* or *Rattus*) and tree shrew (*Ptilocercus*) in the analysis would have resulted in a phylogeny in which Rodentia, Scandentia (tree shrews), and Chiroptera *each* appear as

paraphyletic or polyphyletic groups—clearly unacceptable results. If Rodentia and Scandentia are both monophyletic (hypotheses strongly supported by other morphological and molecular data sets [e.g., Luckett and Hartenberger, 1985; Zeller, 1986]), the hypothesis of bat relationships supported by Pettigrew et al. (1989) minimally requires either independent evolution of a highly organized visual system within each group (e.g., rodents, tree shrews, primates, and megachiropterans) or loss of organization in some members of each. Whichever hypothesis is favored, the potential homoplasy raises strong doubts about the wisdom of considering only characters of the visual neural system in a phylogenetic analysis.

Characters of the visual neural system represent only a small portion of the morphological data that can be brought to bear on the question of chiropteran monophyly. Suthers and Braford (1980:343), who were among the first workers to consider characters of the visual system in bats, cautioned that

Because of mosaic evolution, no single organ system, like the central nervous system, or subsystem, like the visual system, can be relied on alone in attempts to establish phylogenies.

As we have already discussed, previous authors have cited derived features of the dentition, skull and postcranial skeleton, vascular system, musculature, flight membranes, penis, fetal membranes, and non-visual components of the nervous system that must be considered in any analysis of bat relationships (e.g., Koopman and MacIntyre, 1980; Luckett, 1980; Smith and Madkour, 1980; Wible and Novacek, 1988). Pettigrew et al. (1989) appear to feel strongly that the visual neural system is less subject to homoplasy than are these other systems, but such an assumption cannot be supported without testing. Simultaneous cladistic analysis of *all* of the relevant morphological details is the only way that assumptions about homoplasy levels can be replaced with supported hypotheses.

If Pettigrew et al. (1989) are correct in

their hypothesis that primates, dermopterans, and megachiropterans share homologous derived conditions of the visual neural system indicating a close phylogenetic relationship, it is still not clear why Microchiroptera must be excluded from this group. Absence of derived features of the visual system in microchiropterans might be explained as secondary loss (reversal) related to the evolution of sophisticated echolocation and an associated shift from reliance on visual to auditory senses. Secondary loss of derived features of the visual system has already been suggested for odontocete cetaceans (Sanderson, 1986), which have a "primitive" nonlaminated dorsal lateral geniculate nucleus and appear to lack the bilateral retinogeniculate projections apparently characteristic of all other mammals (Kruger, 1959; Jacobs et al., 1975; Sanderson, 1986). It is interesting to note that odontocetes are the only other mammals known to rely on a sophisticated echolocation system comparable to that of microchiropterans, strengthening an argument that reversal may occur in the visual system when other senses (e.g., auditory) are emphasized. Reversals far greater than these are well accepted as explanations for the morphology of blind cave populations of fishes and amphibians, many of which have greatly reduced eyes.

#### BIOCHEMICAL DATA

Studies of amino acid and DNA sequences can provide additional (and potentially independent) sources of data that may address the issue of chiropteran monophyly. Unfortunately, biochemical studies have yet to provide the resolution necessary to choose unequivocally between the two competing hypotheses of bat origins. These results may be attributed both to experimental design (studies that have not been properly designed to discriminate between the two hypotheses) and to the relationship between rates of molecular evolution and timing of morphological change.

Our interpretation of the available molecular data is that they clearly do not refute bat monophyly. Pettigrew et al. (1989: their Fig. 16) presented three trees based

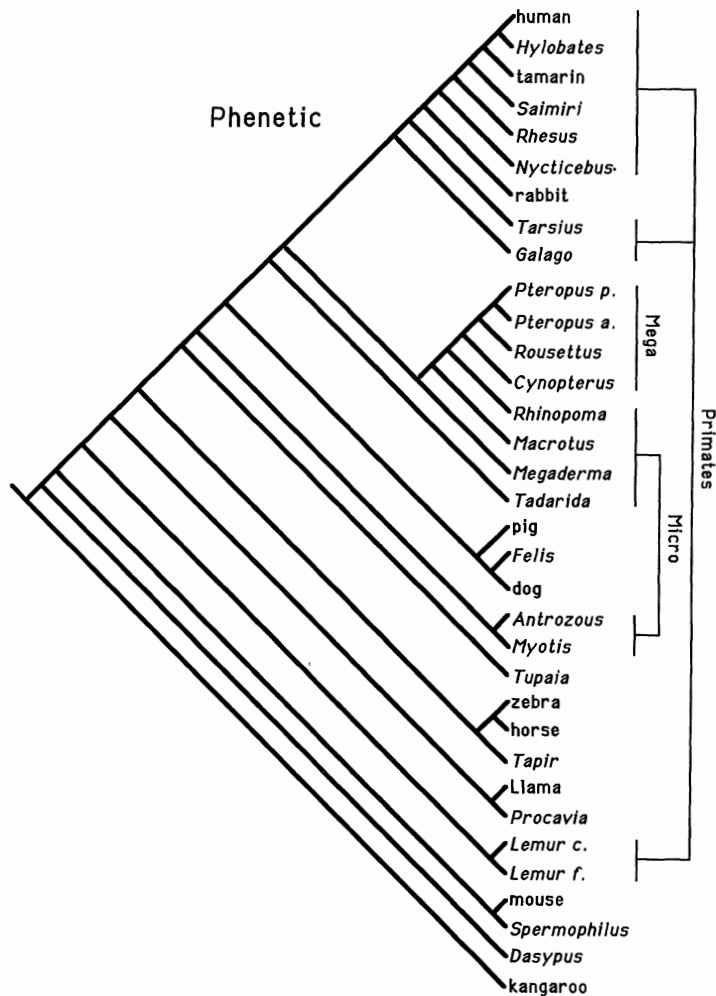


FIGURE 2. Phylogenetic tree based on phenetic similarity of  $\beta$ -globin amino acid sequence data. Modified from Pettigrew et al. (1989: their Fig. 16a).

on analysis of  $\beta$ -globin chains, each of which included 34 species from 12 orders (Figs. 2-4). Two of these trees (one phenetic and one cladistic; Pettigrew et al., 1989: their Figs. 16a, c; our Figs. 2, 3) were generated directly from amino acid sequence data. The third tree (Pettigrew et al., 1989: their Fig. 16b; our Fig. 4) was generated by algorithms that first infer the DNA sequence from the amino acid sequence data and then use the reconstructed DNA sequence to build the tree. One observation concerning these trees is of particular relevance to the current discussion:

in all three trees, the sister taxa of Megachiroptera are three genera of microchiropterans, *not* primates. Interestingly, other microchiropteran genera do not group with these taxa, instead appearing elsewhere in the tree.

If the  $\beta$ -globin chain provides any resolution to mammalian phylogeny, then at least some microchiropterans shared a common ancestor with Megachiroptera after diverging from the lineage that gave rise to most primates. While admitting that the results of the hemoglobin sequence analyses cannot be regarded as definitive,

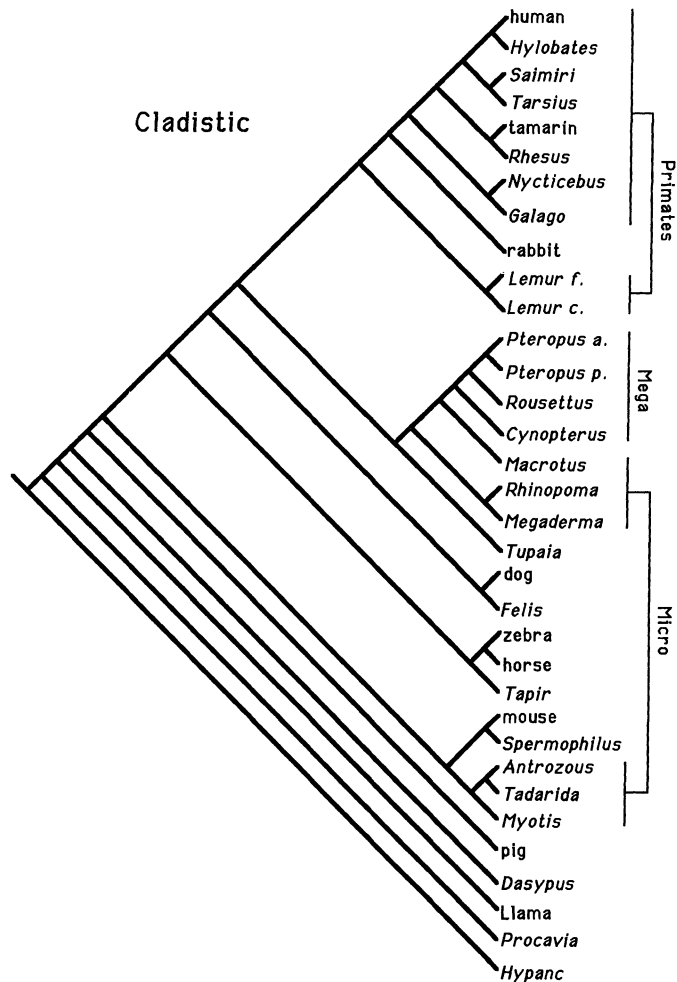


FIGURE 3. Phylogenetic tree based on cladistic resemblance of  $\beta$ -globin amino acid sequence data. Modified from Pettigrew et al. (1989: their Fig. 16c).

Pettigrew et al. (1989:541) nevertheless interpreted these trees as providing some support for their hypothesis:

There is a clear and strong association between megabats and primates. The only non-primate taxon that associates more strongly with primates than the megabats is the rabbit.

Our examination of the  $\beta$ -globin trees indicates a somewhat different conclusion: if bats evolved twice, the hemoglobin data indicate that the split occurred somewhere *within* the group we recognize as Microchiroptera—one group of microchiropter-

ans forming a monophyletic group together with Megachiroptera, the other group of microchiropterans having evolved independently. Interestingly, the group Primates similarly does not appear to be monophyletic in any of the hemoglobin trees—rabbits always fall within Primates (Pettigrew et al., 1989: their Fig. 16), and lemurs frequently appear to be less closely related to anthropoid primates than are all the bats (Pettigrew et al., 1989: their Figs. 16a, b; our Figs. 2, 4). As monophyly of Primates (at least the living taxa) and of Microchiroptera are two issues that are not

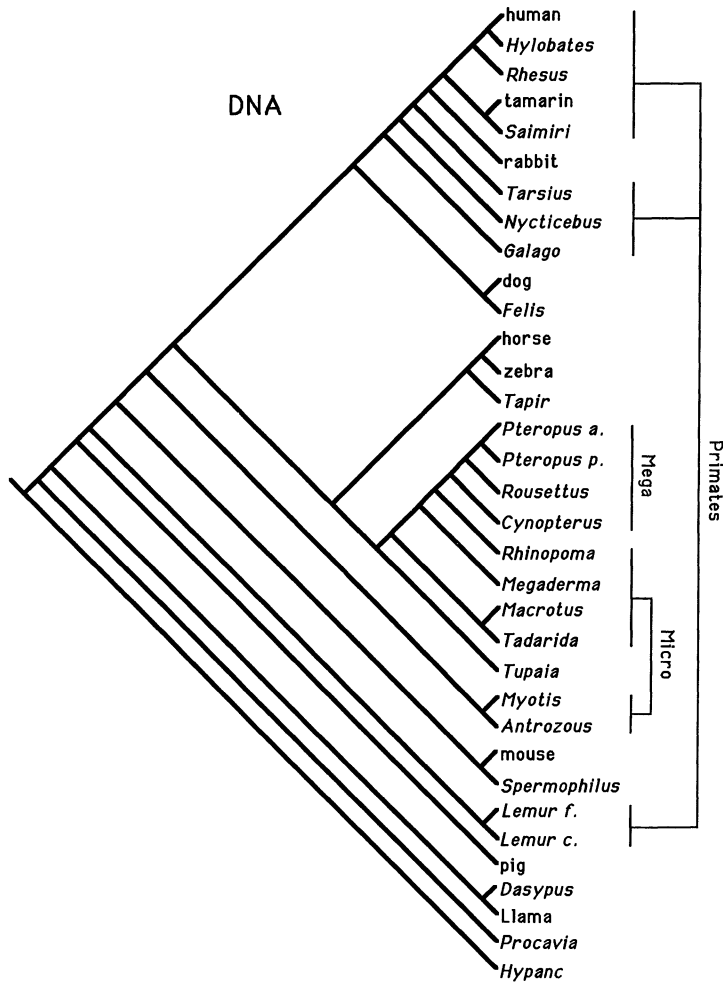


FIGURE 4. Phylogenetic tree based on DNA sequences inferred from  $\beta$ -globin amino acid sequence data. Modified from Pettigrew et al. (1989: their Fig. 16b).

in contention, it is not clear how these hemoglobin data can be considered particularly relevant to the issue of chiropteran monophyly.

One of the problems with using molecular studies to address the relationships among microchiropterans, megachiropterans, and primates is that most previous studies have not been designed (in terms of ingroup and outgroup sampling) to properly resolve alternative patterns of relationship. One exception is a recent study based on restriction maps of the ribosomal DNA cistron (Baker et al., in press). In this

study, 52 restriction sites were mapped for 5 genera of megachiropterans, 13 microchiropterans (representing 13 different families), 1 dermopteran, and 2 primates (*Homo* and *Lemur*). Three outgroups were examined in addition to these taxa, including a mole, a shrew, and a rodent (Baker et al., in press). Unfortunately, cladistic analysis of the restriction sites not only failed to provide clear resolution of the relationships among microchiropterans, megachiropterans, and primates, but this analysis also did not find any clear synapomorphies supporting monophyly of Mi-

crochiroptera (a result similar to that of the hemoglobin studies discussed above). Baker et al. (in press) were forced to conclude that a large number of homoplastic events had occurred and that one potential reason for the poor resolution might involve the time frame of divergence of the extant bat lineages.

If the extant families or superfamilies of bats were established in an explosive adaptive radiation very soon after isolation of their lineage from those of other placental mammals, these groups of bats would have experienced only a short period of common ancestry (perhaps only a few million years) prior to a long period (tens of millions of years) of divergence. A great deal of morphological change may have occurred during this short period of common ancestry, but there is no reason to expect that molecular change occurred at a similar rate. Various parts of the genome evolve at different rates. Relatively rapidly evolving sequences might incorporate sufficient change to document a short period of common ancestry, but continued rapid evolution during the subsequent long periods of genetic isolation would "swamp out" this biochemical record of shared history. In contrast, relatively conservative sequences might remain unchanged during long periods of isolation, but their intrinsically slow rates of change would make it highly unlikely that such sequences would record apomorphies documenting a relatively short period of common ancestry. This suggests that it may be extremely difficult to resolve phylogenetic relationships among lineages produced in a burst of morphological change that occurred many millions of years ago. Baker et al. (in press) predicted that if this explanation is accurate with regard to bats, future molecular studies will encounter the same lack of resolution at the base of the chiropteran phylogenetic tree.

#### CHROMOSOMAL DATA

Chromosome structure may also provide evidence that bears upon the issue of bat monophyly. Pettigrew et al. (1989:493) pointed out that there is a difference in the

frequency and types of chromosomal rearrangements observed in Megachiroptera and Microchiroptera, and that the megachiropteran type of change ("low degree of change; heterochromatic additions most common type of rearrangement") is also seen in primates. However, rates and types of changes are not uniform within primates, and the magnitude of difference between megachiropterans and microchiropterans is no greater than that frequently observed between families (and sometimes even closely related genera) of microchiropterans and other mammals (Baker and Bickham, 1980; Baker et al., 1988). In our opinion (and all of the bat karyotype data cited by Pettigrew et al. [1989] were generated in Baker's lab), the cited differences between Megachiroptera and Microchiroptera are so common between closely related groups that these differences can have no real bearing on the debate at hand. However, other published data do speak to the question of bat monophyly.

Qumsiyeh and Baker (1985) found five chromosomal arms that are shared between rhinopomatid microchiropterans (*Rhinopoma*), the proposed primitive karyotype for phyllostomid microchiropterans (the arms are found in *Macrotus*, among others), and the megachiropteran *Rousettus*. These chromosomal arms, which are identified by G-banding, are not detectable in any published primate karyotype. Qumsiyeh and Baker (1985) proposed that the arms shared by the bats listed above are primitive for all bats; it is possible that they represent synapomorphies of a monophyletic Chiroptera.

#### THE FOSSIL RECORD AND DIVERGENCE TIMES

What may be the most reasonable explanation for all of the morphological and molecular data reviewed above is a hypothesis christened the "blind cave bat scenario" by Pettigrew et al. (1989:548). This hypothesis suggests that the specialized visual system shared by megachiropterans and microchiropterans is actually ancestral for primates and *all* bats; bats are monophyletic, and lack of certain visual spe-

cializations in microchiropterans reflects secondary loss associated with the evolution of their unique echolocating system. Pettigrew et al. (1989:549) rejected this scenario principally because it is apparently contradicted by the fossil record and by gross estimates of divergence time based on hemoglobin sequence data.

The earliest microchiropterans (e.g., *Icaronycteris*) clearly date back to at least the early Eocene, approximately 50 million years ago (Novacek, 1985). In contrast, the earliest presumed megachiropteran is *Archaeopteropus*, which is only 30 million years old (Habersetzer and Storch, 1987). Pettigrew et al. (1989) interpreted the differences in these dates of first occurrence as evidence that Microchiroptera evolved at least 20 million years before Megachiroptera, suggesting that these taxa could not have shared a flying ancestor. What Pettigrew et al. (1989) failed to mention is that the fossil record of bats, particularly megachiropterans, is very patchy. Only two specimens attributed to Megachiroptera predate the Pleistocene—one Oligocene skeleton (*Archaeopteropus*) and one jaw with teeth (*Propotto*) from the Miocene. Megachiropterans clearly are not often fossilized, so there is no reason to believe that *Archaeopteropus* was the "first" megachiropteran. The evidence at hand merely suggests that microchiropterans are very ancient; it does not preclude the possibility that Megachiroptera and Microchiroptera share an even more ancient common ancestor.

Pettigrew et al. (1989) also cited rates of divergence in hemoglobin sequences as supporting a much younger origin for megachiropterans. Even supposing existence of a molecular clock (an assumption strongly questioned by many molecular biologists [e.g., Scherer, 1990]), the data presented by Pettigrew et al. (1989) are not adequate to support their contention that the megachiropteran and microchiropteran lineages originated at different times. Among other things, no member of MacroGLOSSINAE (nectar-feeding megachiropterans) was included in the hemoglobin study; as the basal divergence within Megachi-

roptera may be between Pteropodinae and MacroGLOSSINAE (Anderson, 1912), this omission could have a large effect on estimated times of divergence within Megachiroptera.

#### CONCLUSIONS

Examination of the data and arguments presented by Pettigrew et al. (1989) leads us to conclude that a strong case for diphyly of bats has *not* been established. It is clear that chiropteran relationships present a complex problem that will require further study of both molecular and morphological data. We urge that appropriate sampling, careful analysis, and objective assessment of *all* of the available data be part of all studies concerned with chiropteran monophyly (or any other phylogenetic problem, for that matter). Explicit enumeration of methods and underlying assumptions is also necessary. It is important to present both the strengths and weaknesses of phylogenetic hypotheses. In complicated cases, acceptance of any hypothesis often depends upon permitting other systematists to draw their own conclusions from the evidence at hand.

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## A Fruitful, Wrong Hypothesis? Response to Baker, Novacek, and Simmons

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The opposing viewpoint presented by Baker, Novacek, and Simmons (1991 [this volume]) has concentrated on possible flaws in one of my earlier papers. They have presented to readers neither a coherent account of the strengths of their argument that bats are monophyletic nor any new evidence to support it. In contrast, I have put forward a working hypothesis whose heuristic value is evident from the successful predictions flowing from it, such as

the many new primateline features found in megabats but not in microbats. These new features linking megabats and primates form a growing list—in motor system (Kennedy et al., 1987; Nudo and Masterton, 1990), hippocampus (Buhl and Dann, 1990, 1991), somatosensory cortical representations (Calford and Krubitzer, 1990; Calford and Tweedale, 1990), extrastriate visual cortical areas (Krubitzer and Calford, 1990), and distal limb skele-