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Cranial Evidence for the Monophyletic Origin of Bats

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ABSTRACT

Six derived features of the developing and adult cranium, which are either unique or very unusual in their distributions among mammals, are identified for the two groups of modern bats, megachiropterans (Old World fruit bats) and microchiropterans (echolocating bats). These, combined with the 16 derived features of the postcranial

anatomy and fetal membranes cited in previous studies, strongly support the inclusion of mega- and microchiropterans within the single order Chiroptera and are not congruent with the recent hypothesis that megachiropterans (and dermopterans) are more closely related to primates.

INTRODUCTION

Wings for powered flight are generally regarded as the major feature uniting the two suborders of modern bats, Megachiroptera (Old World fruit bats) and Microchiroptera (echolocating bats), within the Order Chiroptera (Gregory, 1910; Simpson, 1945; Novacek, 1980b). Challenges to chiropteran monophyly have appeared previously (Smith, 1976, 1977; Smith and Madkour, 1980; Hill and Smith, 1984), but the most provocative is that of Pettigrew (1986). He argued that flight has been acquired independently in the

two bat suborders and that megachiropterans are an early branch of primates. According to Pettigrew, support for his hypothesis is threefold: (1) mega- and microchiropterans share no derived characters other than those related to flight; (2) mega- and microchiropterans exhibit differences in the flight apparatus; and (3) megachiropterans share derived characters with primates not found in microchiropterans. More recently, Pettigrew and Cooper (1986) reported that the derived characters shared by primates and megachi-

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ropterans also appear in dermopterans (gliding lemurs or colugos). They concluded (p. 1035) that "an early branch of the primates gave rise to the dermopterans (gliding lemurs) some of which developed true flight to give rise to the megachiropterans."

Of the three observations offered by Pettigrew (1986) in support of his hypothesis, the latter two are not contestable. That there are, in addition to numerous similarities, small skeletal and muscular differences in the wings of mega- and microchiropterans is well known (Strickler, 1978; Smith and Starrett, 1979). Yet, these differences do not necessarily argue for convergent acquisition of flight; they may merely be unique specializations of mega- and microchiropterans within the Order Chiroptera. In fact, some differences in the flight apparatus are not unexpected, given that the two suborders have been separated for at least 50 million years (Novacek, 1985). That there are derived characters of the visual pathways which megachiropterans share with primates (and dermopterans) is also not arguable. But it is not certain why these characters should be given more weight in delimiting natural groups of organisms than some others. Why is convergent acquisition of certain visual pathways "less likely than independent evolution of flight in two groups of mammals" (Pettigrew and Cooper, 1986, p. 1035)?

Pettigrew's (1986) other observation supporting bat diphyly, that there are no derived characters shared by mega- and microchiropterans other than those related to flight, is contestable. In an analysis of higher-level relationships within Eutheria, Novacek (1982) identified 16 derived characters shared by the two suborders in support of bat monophyly. Most characters involve the postcranium and are arguably flight adaptations, but three are from the fetal membranes and two from the cranium. Pettigrew (1986) rejected these five "non-flight" characters as equivocal. He correctly pointed out that the fetal membrane characters appear in other eutherians, but speculated without explanation that the cranial characters may be primitive rather than derived states.

Because of Pettigrew's (1986) objections and the provocative nature of his hypothesis, we review here the cranial evidence for the

monophyletic origin of bats. We present a detailed justification for the polarity assignment of the cranial characters previously identified by Novacek (1982). In addition, we report new evidence from the developing and adult cranium that supports Chiroptera as a monophyletic taxon. Finally, we evaluate the plausibility of diphyletic and monophyletic origins for bats in light of the distribution of the various anatomical features supporting these two views.

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ABBREVIATIONS

Anatomical

as	alisphenoid
at	auditory tube
bo	basioccipital
bs	basisphenoid
ce	caudal entotympanic
co	cochlea
ct	cavum tympani
e	ectotympanic
eo	exoccipital
i	incus
ica	internal carotid artery
m	malleus
mx	maxilla
n	nasal
pmx	premaxilla
pr	promontorium of petrosal

re	rostral entotympanic
ri	ramus inferior of the stapedial artery
rs	ramus superior of the stapedial artery
sa	stapedial artery
sq	squamosal
t	tensor tympani muscle
tt	tegmen tympani

Institutional

AIF	Anatomisches Institut, Frankfurt am Main
AIG	Anatomisches Institut, Göttingen
AM	American Museum of Natural History, Department of Mammalogy
AMNH	American Museum of Natural History
CA	American Museum of Natural History, Comparative Anatomy Collections
DUCEC	Duke University Comparative Embryology Collection
UCC	Department of Anatomy, University College, Cardiff

Embryological Measures

CRL	crown-rump length (vertex to breech)
HL	head length (greatest length between tip of nose and rear of skull)
ST	section thickness

METHODS AND MATERIALS

Central to our analysis are two methodological issues raised by Pettigrew (1986): the determination of character polarity and the assignment of character weighting. These issues have been the subject of much debate in recent years, and the approach we employ is presented below.

The two most popular methods for determining the evolutionary polarity of characters—their primitive (plesiomorphous) and derived (apomorphous) states—are the ontogenetic method (Nelson, 1978) and the outgroup method (Maddison et al., 1984). The ontogenetic method is not really applicable here because developmental sequences of cranial characters are not known in detail for most bats. Developmental data are used in our analysis, but we follow De Queiroz (1985) and treat ontogenetic transformations as characters themselves. To determine polarity, we employ the outgroup method, which assumes that the primitive state of a character is that found in the closest relatives of the group under study. As a drawback, this method assumes that outgroup relationships are

well resolved. Although there have been advances recently in resolving the branching pattern of the eutherian ordinal tree (Novacek, 1986; Novacek and Wyss, 1986), relationships among bats, primates, and their allies are not well resolved (Wible and Covert, 1987). Therefore, we do not limit discussion to some portion of the eutherian ordinal tree, but examine the distribution of characters across all Recent eutherian orders and, where possible, selected fossil groups, before assigning polarity.

Shared derived characters (synapomorphies) are the only basis for delimiting natural groups of organisms (monophyletic groups or clades) (Hennig, 1966), but not all synapomorphies are equally reliable as indicators of phylogenetic affinity. Some characters are more likely to arise independently and more often than others. To reflect the varying evolutionary significance of shared similarities, some authors (Hecht, 1976) suggest a priori weighting of characters. We follow a less formal approach here and hold that the distributions of the characters themselves are the basis for weighting (Patterson, 1982; Novacek, 1986). Emphasis is placed on those characters delimiting monophyletic groups that repeatedly resist contradiction in tests with additional characters. In contrast, characters that appear in apparently unrelated taxa or that face strong contradiction in tests with additional characters are of low weight. We, furthermore, have more confidence in characters whose distributions are known across a wide range of taxa, rather than characters known for only a few forms from a few orders.

Skulls of the 41 Recent genera of megachiropterans and of representatives of the 16 Recent families of microchiropterans (see Koopman, 1984) were studied in the collections of the Department of Mammalogy of the American Museum of Natural History, the Department of Zoology of the British Museum (Natural History), and the Division of Mammals of the Field Museum of Natural History. In addition, serially sectioned crania from embryonic, fetal, and postnatal developmental stages were studied in several embryological collections (table 1). Comparisons were made with skulls from representatives of all Recent mammalian orders and with serially sectioned crania from represen-

TABLE 1
Chiroptera: Sectioned Specimens

Specimens		CRL (mm)	HL (mm)	ST (μm)	Stains
Megachiroptera					
Pteropodidae					
<i>Rousettus leschenaulti</i>					
AIF 1	embryo	15	—	14	azan
<i>Rousettus aegyptiacus</i>					
AIF 87	fetus	32	—	30	azan
<i>Hypsignathus monstrosus</i>					
AIG E2150	fetus	—	—	40	azan
<i>Pteropus</i> sp.					
DUCEC 831	fetus	93.5	—	16	mallory
<i>Pteropus medius</i>					
AIF 116-117	newborn	—	—	80, 100	azan
Microchiroptera					
Rhinolophidae					
<i>Hipposideros puttalam</i>					
UCC Hi 3	embryo	8	—	10	masson
UCC Hi 2	embryo	10	—	10	masson
UCC Hi 1	embryo	13	—	10	masson
Vespertilionidae					
<i>Miniopterus schreibersi</i>					
AIF S/Ch 341	embryo	9	—	10	hematoxylin/azocarmine
<i>Myotis myotis</i>					
AIF S/Ch 344	embryo	9	—	10	hematoxylin/azocarmine
AIF 1.2.51	embryo	12	7	12	hematoxylin/azocarmine
AIF 1.10.50	embryo	12	8	12	azan
AIF 1.9.50	fetus	14	9	12	azan
AIF 1.3.51	fetus	15	10	—	azan
AIF 15.6.49	fetus	18.3	13	15	azan
AIF 1.2.49	fetus	21	14	12	azan
AIF 1.1.49	fetus	22	15	12	azan
AIF 17.5.49	fetus	30	—	15	azan
AIF S/Ch 353	adult	—	—	30, 35	azan
<i>Pipistrellus pipistrellus</i>					
UCC Hi 4	fetus	16.5	10.1	10	masson
Molossidae					
<i>Tadarida</i> sp.					
UCC SB 45	fetus	18	—	10	masson
<i>Tadarida pumila</i>					
UCC Ch 1	fetus	29	16	10	masson

tatives of all orders except Perissodactyla, Hyracoidea, Proboscidea, Sirenia, and Tubulidentata, for which specimens were not available. We have been independently studying extinct and extant mammalian crania for several years, and we utilized lists of cranial character distributions that we have

presented elsewhere (Novacek, 1980a, 1986; Wible, 1984, 1987).

RESULTS

The following derived cranial characters are shared among all (or nearly all) mega- and

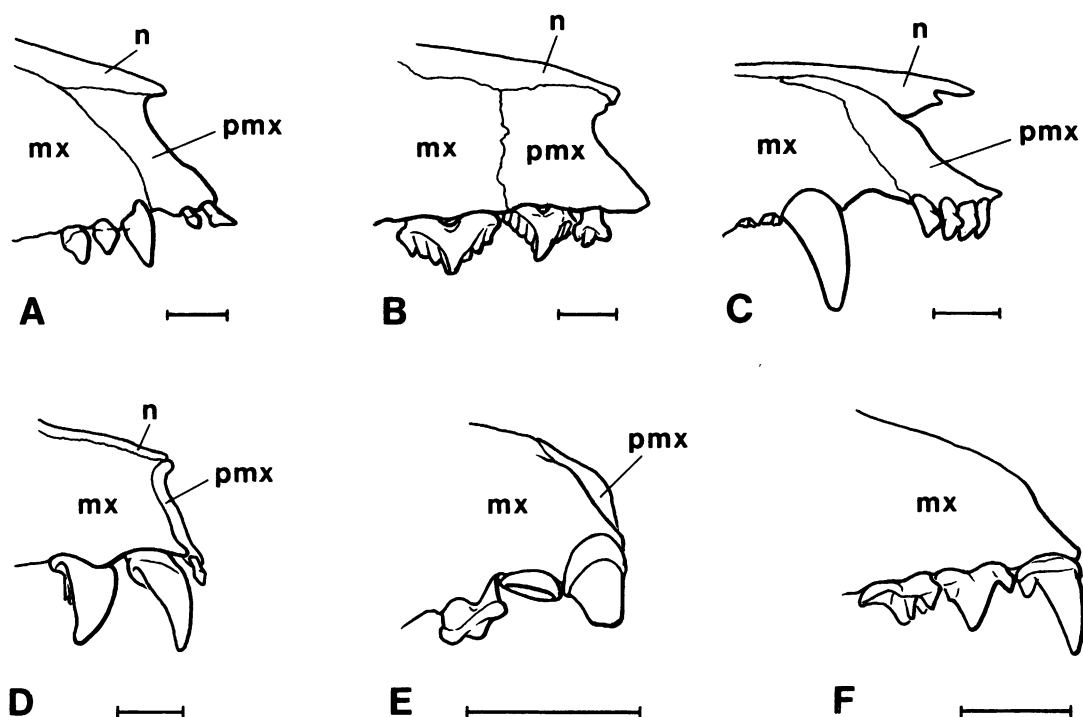


Fig. 1. Lateral views of right skull rostrum in: (A) the Eocene euprimate *Notharctus osborni* AMNH 11466; (B) the dermopteran *Cynocephalus* sp. CA 3633; (C) the marsupial *Didelphis marsupialis* AM 2394; (D) the megachiropteran *Dobsonia moluccensis* AM 198750; (E) the emballonurid microchiropteran *Taphozous flaviventris* AM 107759; (F) the megadermatid microchiropteran *Macroderma gigas* AM 162673. Scale bars equal 5 mm. A small nasal process of the premaxilla is present in *Macroderma gigas*, but is not visible in lateral view.

microchiropterans and are also unique (or very unusual) in their distribution among other mammals.

(1) *Premaxilla is greatly reduced* (Novacek, 1982).

Typically in mammals, the premaxilla is a well-developed element of the anterior rostrum (fig. 1A, B, C). It is broadly exposed rostrally around the external nares and on the palate, where it both surrounds the incisive foramina and forms a median septum between these paired openings. This condition appears in marsupials and all modern eutherian orders except Chiroptera. (Secondary reductions of the premaxilla have occurred in some edentates and primates [see below].)

Bats exhibit considerable interspecific variation in the development of the premaxilla, and this has been shown to be of great taxonomic significance in recognizing lower-level relationships within the order (Miller,

1907). Yet, the chiropteran premaxilla is always markedly reduced (fig. 1D, E, F). In megachiropterans, the palatal processes are lacking or greatly reduced and the paired nasal processes fail to form more than a weak contact anterior to the single opening for the incisive foramen (except *Nyctimene*, *Paranyctimene*, and *Harpyionycteris*, where the premaxillae are nonetheless very small). In microchiropterans, the premaxillae are either (1) entirely absent (some megadermatids), (2) have a well-defined (but small) nasal process, with the palatal process absent or very incomplete (some megadermatids, Rhinopomatidae, Craseonycteridae, Emballonuridae, Noctilionidae, Furipteridae, Vespertilionidae), (3) have only a well-defined (but small) palatal process (Nycteridae, Rhinolophidae), or (4) have weak nasal and palatal processes (Phyllostomatidae, Natalidae, Thyropteridae, Myzopodidae, Mystacinidae, Molossi-

dae). Only in Mormoopidae is the nasal process of the premaxilla well developed, but this appears to be related to the anomalous inflation of the nasal region and is undoubtedly a secondary condition.

Although no other order of mammals shows such a marked reduction of the premaxilla as a generalized condition, this element has been secondarily reduced within the Orders Edentata and Primates. Among edentates, the sloths (bradypodids) and anteaters (myrmecophagids) have a greatly reduced premaxilla. These forms are generally united (Simpson, 1945; Engelmann, 1985) in the suborder Pilosa, and their reduced premaxilla distinguishes them from the armadillos (dasypodids), which exhibit the general therian condition of the premaxilla. Among primates, most modern taxa show some degree of reduction to the premaxilla, but this bone is large in Paleogene euprimates (adapids and omomyids) and in plesiadapoids, the forms generally held (Szalay and Delson, 1979) to be the sister-group to the euprimates (for an opposing view, see Wible and Covert, 1987).

(2) *Jugal is greatly reduced* (Novacek, 1982).

Nearly all mammals have a large jugal that occupies the greater part of the zygoma and has a dorsal process that forms the antero-ventral rim of the orbit and contacts the lacrimal. In contrast, the jugal in mega- and microchiropterans is confined to the mid-face region of the zygomatic arch and well separated from contact with the lacrimal by the zygomatic process of the maxilla. This pattern is not unique to bats: the jugal is reduced in erinaceomorph lipotyphlans and lagomorphs and is totally absent in pholidotans and soricomorph lipotyphlans. Yet, it seems unlikely that these cases are homologous with the condition in chiropterans. Well-developed jugals occur in the nearest relatives of lipotyphlans and lagomorphs, whether one follows evidence from morphology (Novacek, 1986) or molecules (Miyamoto and Goodman, 1986), and the total absence of the jugal in pholidotans and soricomorph lipotyphlans is a highly anomalous feature.

(3) *The tegmen tympani tapers to a slender process that projects ventrally into the middle-ear cavity medial to the epitympanic recess.*

The tegmen tympani is a neomorphic ele-

ment on the auditory capsule in the therian chondrocranium (Kuhn and Zeller, 1987). It projects anteriorly from the crista parotica, to which the second branchial arch cartilage (Reichert's cartilage) is usually fused, and contributes to the roof of the epitympanic recess, the dorsal extension of the middle-ear cavity that lies above the level of the tympanic membrane and contains the incudomalleolar articulation. Absent in monotremes and rudimentary in marsupials (Kuhn and Zeller, 1987), the tegmen tympani is moderately well developed in nearly all eutherians, projecting far anteriorly from the crista parotica and contributing substantially to the closure of the roof of the middle-ear cavity (fig. 2A). Typically, the eutherian tegmen tympani abuts on (or sometimes fuses with) the lateral surface of the pars cochlearis of the auditory capsule (the chondrocranial precursor of the promontorium of the petrosal) and stretches laterally to contact the squamosal. It overlies the tensor tympani muscle and along with the squamosal forms a roof over the epitympanic recess. Variants on the general eutherian pattern occur in pholidotans and dermopterans, in which the tegmen tympani is greatly reduced and the roof of the epitympanic recess is completed by the squamosal; and in euprimates, scandentians, rodents, lagomorphs, and macroscelideans, in which the tegmen tympani is expanded laterally and there is little or no squamosal contribution to the roof of the epitympanic recess (MacPhee, 1981; Wible, unpubl. obs.).

The most unusual variant on the general eutherian pattern is that of chiropterans. This was first observed in a fetus of the vespertilionid *Miniopterus schreibersi* by Fawcett (1919). He stated (p. 324) that "the tegmen tympani projects forwards and downwards with a curious sinuous course. It finally bends inwards towards the 'cochlear' segment of the pars cochlearis and ends in a pointed extremity." Since then, this unusual pattern has been described and/or figured for prenatal specimens of the pteropodid *Rousettus* (Klaauw, 1922; Jurgens, 1963; Wible, 1984), the rhinolophid *Rhinolophus rouxii* (Sitt, 1943), and the vespertilionids *Scotophilus temmincki* (Koch, 1950) and *Myotis myotis* (Frick, 1954; Wible, 1984). We add here our observations

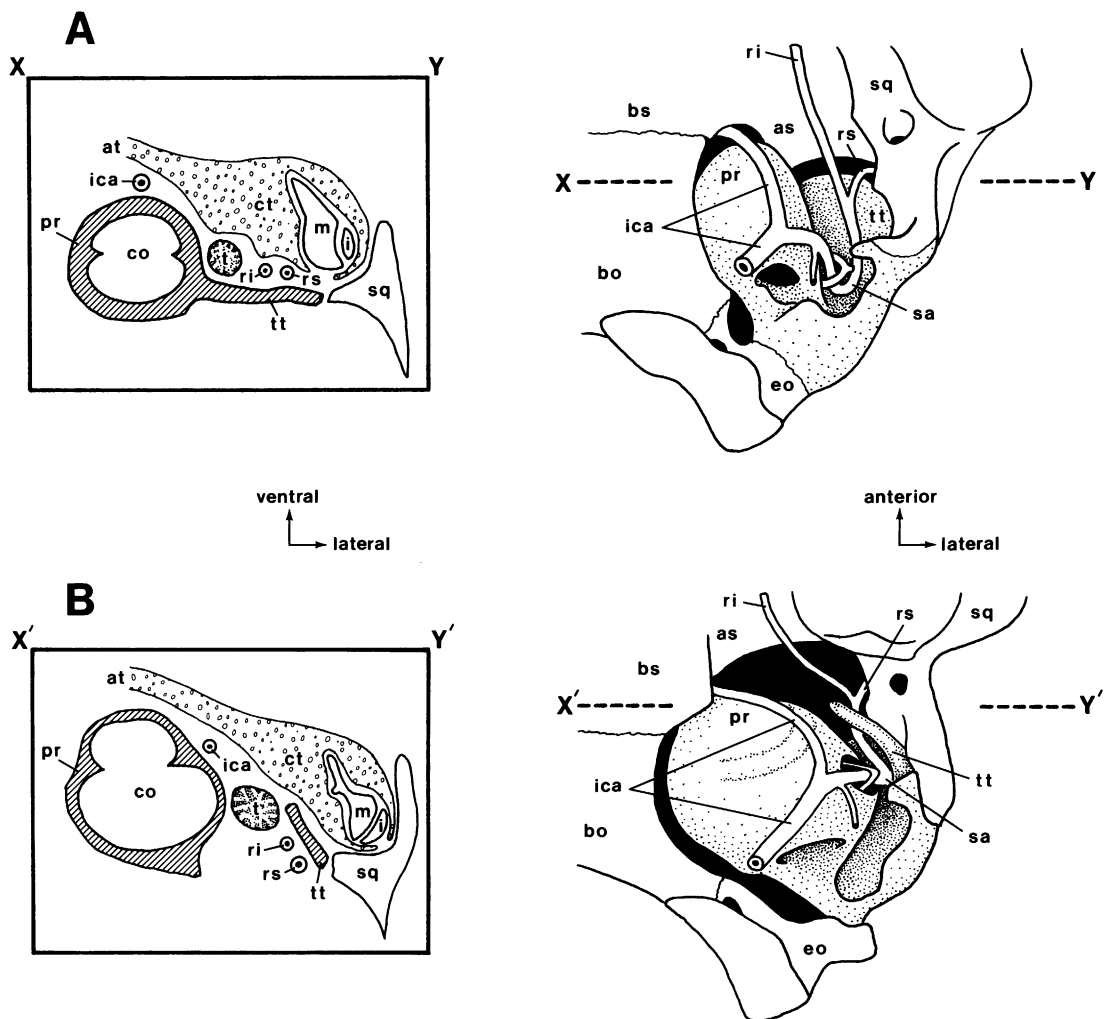


Fig. 2. Auditory regions of (A) a hypothetical ancestral eutherian and (B) a bat (the vespertilionid microchiropteran *Myotis myotis* AIF S/CH 353). In ventral view (right side), the auditory bulla, cavum tympani, malleus, incus, and ossicular muscles (tensor tympani and stapedius) are removed to expose the internal carotid artery and its branches on the petrosal bone (stippled). In cross section along planes XY and X'Y' respectively (left side), the cavum tympani, malleus, incus, and tensor tympani muscle are included.

on the serially sectioned specimens listed in table 1. In all these mega- and microchiropterans, the tegmen tympani tapers to a slender process at its rostral extent and projects ventrally (and somewhat medially) into the middle-ear space (fig. 2B). It does not form a roof over the tensor tympani muscle and epitympanic recess as in other eutherians, but lies between the two, forming the lateral wall of a fossa for the muscle and the medial wall

of the epitympanic recess. Because the ventral projection of the tegmen tympani is very delicate, it is frequently broken in macerated adult skulls. Nonetheless, we have identified this bony process in museum specimens for representatives of all 17 bat families. The extent of this projection is generally greater in microchiropterans, with the most extreme rostral elongation in molossids, in which the tegmen reaches the alisphenoid.

The chiropteran tegmen tympani is further distinguished from that of other eutherians by its unusual pattern of ossification. Typically in eutherians, the tegmen tympani ossifies as part of the petrosal bone. However, in the late fetal stages of bats that have been studied, only the posterodorsal portion of the tegmen tympani ossifies; the anteroventral portion remains cartilaginous and forms the posterior part of the cartilage of the auditory tube. The cartilage of the auditory tube usually forms from a single center of chondrification in eutherians (MacPhee, 1981; Wible, 1984). The bat tubal cartilage has at least two centers, one of which is the anteroventral portion of the tegmen tympani, that fuse to form the adult structure. This unusual pattern has been described for the pteropodid *Rousettus* (Klaauw, 1922; Wible, 1984) and the vespertilionid *Myotis myotis* (Wible, 1984). To these, we add our observations on the pteropodid *Pteropus*, the vespertilionid *Pipistrellus pipistrellus*, and the molossid *Tadarida*.

The tegmen tympani is fused to an adjacent cartilaginous element in two other mammals, the scandentian *Tupaia* (Cartmill and MacPhee, 1980) and the perissodactyl *Rhinoceros* (Kampen, 1905). However, these forms differ from chiropterans in that the tegmen is fused to an entotympanic, an independent piece of cartilage that contributes to the formation of a closed auditory bulla, and the tegmen and entotympanic co-ossify during development. Furthermore, fusion of the tegmen tympani and entotympanic is absent in the scandentian *Ptilocercus* (Le Gros Clark, 1926; Zeller, 1986) and other perissodactyls (Kampen, 1905) and so, has been acquired independently within Scandentia and Perissodactyla.

The peculiarities of the chiropteran tegmen tympani may be related to the action of the tensor tympani muscle. First of all, the posterior portion of the tubal cartilage, which is derived ontogenetically from the tegmen, affords attachment area for the tensor tympani muscle (Henson, 1970; Wible, unpubl. obs.). Secondly, the ventral projection of the tegmen tympani forms the lateral wall of a partial canal for the tensor tympani muscle (fig. 2B). An osseous semicanal for the tensor tympani muscle also appears in *Homo sapiens*, although it forms in a totally different way via periosteal outgrowths from the coch-

lear capsule (Anson and Donaldson, 1981). This semicanal in humans is thought to act as a pulley to change the direction of action of the muscle (Wever and Lawrence, 1954); the chiropteran tegmen tympani may have a similar function.

(4) *The ramus inferior of the stapedial artery passes through the cranial cavity dorsal to the tegmen tympani.*

The ramus inferior is a primary branch of the mammalian stapedial artery that through its branches supplies the upper and lower jaws (Tandler, 1899; Wible, 1984, 1987). In most eutherians, the ramus inferior arises from the proximal stapedial artery within the middle-ear space and travels forward ventral to the tegmen tympani in company with the lesser petrosal nerve (fig. 2A). An intratympanic course also occurs in the monotreme *Ornithorhynchus*, the only noneutherian mammal with a ramus inferior in the adult, and is taken as the plesiomorphous condition for Eutheria (Wible, 1984, 1987).

The ramus inferior exhibits a different pattern in the serially sectioned bats studied here (table 1): it arises from the proximal stapedial artery within the cranial cavity and runs forward dorsal to the tegmen tympani (fig. 2B). An intracranial course for the ramus inferior is not unique to chiropterans, but also occurs in lagomorphs, rodents, and macroscelideans (Wible, 1984, 1987) and possibly in extinct leptictid insectivorans (Novacek, 1980a, 1986). However, the bat condition differs in that the proximal stapedial enters the cranial cavity medial to the tegmen tympani; the artery in lagomorphs, rodents, and macroscelideans either passes rostral to or through the tegmen tympani (MacPhee, 1981; Wible, 1984). The intracranial ramus inferior of these various forms appears to be the homolog of the intratympanic ramus inferior of other mammals, because both vessels run in company with the lesser petrosal nerve (Wible, 1984, 1987). Either the ramus inferior of bats, lagomorphs, rodents, and macroscelideans has "shifted" dorsal to the tympanic roof or the tympanic roof forms in a more ventral plane relative to the ramus inferior. The latter would support Kuhn's (1971) view that the tegmen tympani (or portions of it) has been added to the tympanic roof independently numerous times in mammals.

(5) *The ramus infraorbitalis of the stapedial artery passes through the cranial cavity dorsal to the alisphenoid.*

The ramus infraorbitalis is a branch of the ramus inferior of the mammalian stapedial artery (or maxillary artery) that originates in front of the tympanic region and runs forward to supply the upper jaws (Wible, 1984, 1987). Two possible pathways through the orbitotemporal region occur among most modern forms: the ramus infraorbitalis either runs ventral to the alisphenoid or it runs through a canal in the alisphenoid. From the distribution of these two character states, we have elsewhere supported the former pathway as primitive for Eutheria (Wible, 1984, 1987; Novacek, 1986).

The mega- and microchiropterans for which the cranial arterial system has been studied exhibit a different course for the ramus infraorbitalis. This vessel enters the cranial cavity through the anterior portion of the foramen ovale (or through a separate opening in front of the foramen ovale), turns forward dorsal to the alisphenoid, and passes into the back of the orbit through the confluent superior orbital fissure/foramen rotundum. An intracranial course for the ramus infraorbitalis is known from dissections, sectioned material, or macerated skulls with intact dried arteries for pteropodine megachiropterans and emballonurid, megadermatid, rhinolophid, phyllostomatid, vespertilionid, and molossid microchiropterans (Tandler, 1899; Grosser, 1901; Buchanan and Arata, 1967; Kallen, 1977; Wible, 1984, unpubl. obs.). The intracranial ramus infraorbitalis apparently is not homologous with the extracranial ramus infraorbitalis of other mammals because the phyllostomatid *Artibeus lituratus* (Buchanan and Arata, 1967) and the molossid *Tadarida* (table 1) have both vessels. The intracranial ramus infraorbitalis is absent in two microchiropterans, the rhinolophid *Rhinolophus* (Grosser, 1901; Kallen, 1977) and the phyllostomatid *Desmodus* (Kallen, 1977), and blood reaches the face via an extracranial artery. We view this absence as a derived state for these forms, because an intracranial ramus infraorbitalis appears in other representatives of these two families.

A ramus infraorbitalis with an intracranial course comparable to that of chiropterans also

occurs in some soricomorph lipotyphlans (Roux, 1947). However, this course has been acquired independently in these forms, because an intracranial ramus infraorbitalis is absent in other soricomorphs and in erinaceomorph lipotyphlans (Tandler, 1899; Roux, 1947).

(6) *Two entotympanic elements appear in the floor of the middle-ear cavity: a large caudal element and a small rostral one grooved by (or forming a canal around) the internal carotid artery.*

In the adults of all living mammals, the floor of the middle-ear space is formed by an auditory bulla, a protective shell composed of membrane, bone, and cartilage in varying proportions. There are only two constant elements of the auditory bulla in modern forms: the ectotympanic bone and the fibrous membrane of the tympanic cavity, a sheet of connective-tissue fibers stretching between the promontorium of the petrosal and the ectotympanic (MacPhee, 1981). In addition to these two constant elements, an array of independent cartilaginous and osseous structures (entotympanics) and outgrowths from surrounding skeletal components (tympanic processes) contribute to the auditory bulla in different mammalian groups (Kampen, 1905; Klaauw, 1931; Novacek, 1977). Because complete, osseous bullae are absent in monotremes, Mesozoic mammals, most Paleogene eutherians, and some modern marsupials and placentals, it is generally held (Novacek, 1977, 1986; Cartmill and MacPhee, 1980; MacPhee, 1981; Wible, 1984) that the auditory bulla was largely membranous in primitive eutherians.

In the fetal bats studied here (table 1) and by Klaauw (1922), Frick (1954), and Jurgens (1963), two separate entotympanic elements preform in cartilage in the floor of the tympanic cavity (fig. 3). A large caudal entotympanic, which may remain cartilaginous in the adult, contributes to the posterior and medial tympanic floor, and a small rostral entotympanic occupies the anteromedial corner of the tympanic floor ventral to the anterior carotid foramen. The development of the latter element differs in the two bat suborders: in microchiropterans, the rostral entotympanic forms from a single piece of cartilage, while the megachiropteran element has several cen-

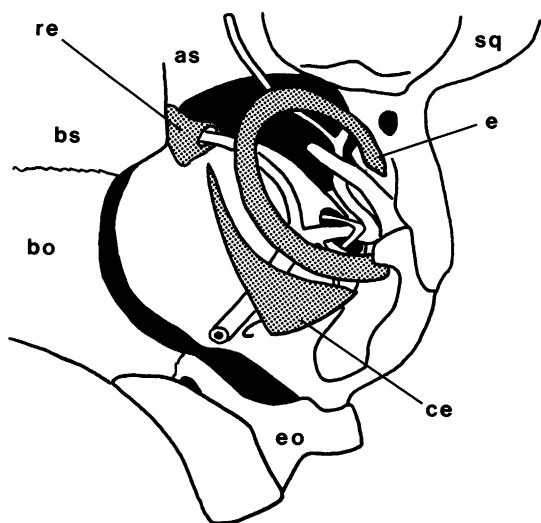


Fig. 3. Auditory region of the vesperilionid microchiropteran *Myotis myotis* shows in the three elements in the floor of the middle-ear space in a late fetal stage (AIF 1.1.49). The intramembranous ectotympanic and the cartilaginous rostral and caudal entotympanics expand in later ontogeny to form the complete osseous auditory bulla of the adult.

ters of chondrification that fuse in later ontogeny. Despite this difference, the rostral entotympanics in the two suborders appear to be homologs, because they occupy the same portion of the tympanic floor and are grooved by (or form a canal around) the internal carotid artery. It is difficult to identify these

various independent bullar elements in skulls of adult bats, because they either have fused seamlessly with the ectotympanic or have fallen out. Rostral and caudal entotympanics in the tympanic floor are not unique to bats; they also occur in Recent carnivorans, dermopterans, macroselideans, and hyracoids (Klaauw, 1922; Cartmill and MacPhee, 1980; Wible, 1984). However, only carnivorans have a large caudal entotympanic and a small rostral entotympanic associated with the internal carotid artery as in chiropterans (Hunt, 1974; Wible, 1984). Because these elements are not known for miacids, the earliest true carnivorans (Matthew, 1909), we infer that they have been acquired independently in Carnivora and Chiroptera.

DISCUSSION

Two contrasting hypotheses of chiropteran relationships are presented in figures 4 and 5. In the diphyly hypothesis (fig. 4), mega-chiropterans are more closely related to dermopterans, primates, and tree shrews than to microchiropterans (following schema presented by Smith and Madkour, 1980, and Pettigrew and Cooper, 1986), and in the monophyly hypothesis (fig. 5), mega- and microchiropterans are more closely related to each other than to the remaining taxa. We evaluate these hypotheses below in light of the distribution of the various supporting anatomical features.

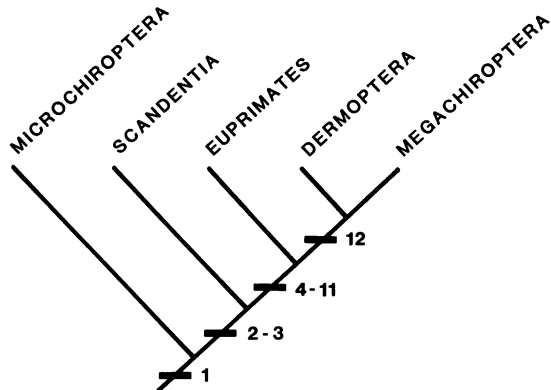


Fig. 4. Cladogram of archontan interrelationships proposed by Smith and Madkour (1980). Numbers refer to characters listed in table 2.

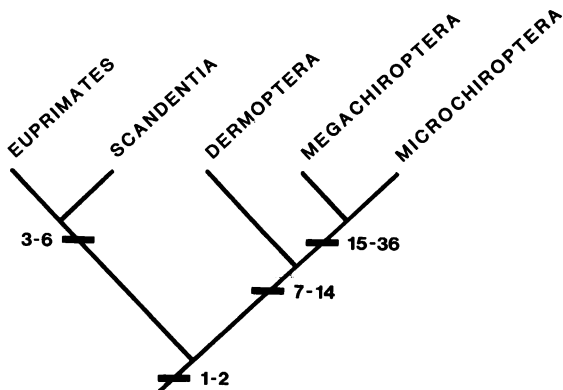


Fig. 5. Cladogram of archontan interrelationships supported here. Numbers refer to characters listed in table 3.

TABLE 2
Derived Characters Proposed by Smith and Madkour (1980) and Pettigrew and Cooper (1986) Supporting Phylogenetic Relationships Shown in Figure 4

1. Free and pendulous penis.
2. Accessory cavernous tissue absent.
3. Enlarged neocortex.
4. Reduced, but binocularly balanced retinotectal pathway subserving only contralateral hemifield of visual space.
5. Ipsilateral retinal input to rostralmost tectum.
6. Ipsilateral bias in retinotectal-hypothalamic pathway.
7. Reduced accessory optic input to medial terminal nucleus.
8. Complex of characters in organization of lateral geniculate nucleus, with segregation of ocular input to different laminae and with magnocellular laminae adjacent to optic tract.
9. Distally expanded, vascular corpus spongiosum.
10. Derived, noninsectivorous dentition.
11. Distal radius and lunate expanded.
12. Patagium for gliding or modified as a wing.

TABLE 3
Derived Characters Reviewed Herein for Support of Phylogenetic Relationships Shown in Figure 5

1. Pendulous penis suspended by a reduced sheath between genital pouch and abdomen.
2. Sustentacular facet of the astragalus in distinct medial contact with distal astragalar facets.
3. Complete postorbital bar.
4. Petrosal-derived osseous canals around intratympanic portions of facial nerve and stapedial artery.
5. Anterior carotid foramen in basisphenoid converted to a long tube.
6. Tegmen tympani expanded anterolaterally to roof epitympanic recess; tegmen tympani with an epitympanic crest within which stapedial artery runs.
7. Fenestra cochleae (round window) faces directly posteriorly.
8. Subarcuate fossa greatly expanded and dorsal semi-circular canal clearly separated from the endocranial wall of the squamosal.
9. Neural spines on cervical vertebrae 3–7 weak or absent.
10. Ribs flattened, especially near their vertebral ends.
11. Forelimbs markedly elongated.
12. Patagium continuously attached between the digits of the manus.
13. Ulna markedly reduced at both its proximal and distal ends.
14. Humeropatagialis muscle inserts into plagiopatagium.

15. Premaxilla greatly reduced.
16. Jugal greatly reduced.
17. Tegmen tympani tapers to a slender process that projects ventrally into the middle-ear cavity medial to the epitympanic recess.
18. Ramus inferior of the stapedial artery passes through the cranial cavity dorsal to the tegmen tympani.
19. Ramus infraorbitalis of the stapedial artery passes through the cranial cavity dorsal to the alisphenoid.
20. 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.
21. Distal end of humerus lacks supratrochlear depression and supinator ridge.
22. Entepicondylar foramen of the humerus absent.
23. Digits 2–5 of manus greatly elongated to support wing membrane.
24. Manus rotated 90° from position typical of quadrupedal mammals.
25. Claws lost from terminal phalanges on digits 3 and 4 of forelimb.
26. Hindlimbs rotated from typical quadrupedal orientation (femur directed laterad and tibia directed caudad during flight and dorsolaterad and ventrad, respectively, during crawl).
27. Trochlea of astragalus lacks medial and lateral marginal ridges.
28. Calcanealastragalar facet of calcaneum modified from convex process to depression or trough.
29. Peroneal tubercle of calcaneum absent.
30. Depressor osseous styloformes muscle runs between calcaneum and calcar.
31. Occipitopollicalis muscle present on the leading edge of propatagium.
32. Sartorius muscle absent.
33. Preplacenta broad and horseshoe-shaped with definitive placenta more localized.
34. Definitive yolk sac “gland-like.”
35. Prominent “interstitial membrane” in the chorioallantoic placenta.
36. Cortical somatosensory representation of forelimb reverse of that in other mammals.

BAT DIPHYLY

The hypothesis of bat diphyly depicted in figure 4 is supported largely by evidence from soft-tissue structures in the central nervous system and penis observable in modern forms only.

(1) *Central nervous system.* In a recent abstract, Pettigrew and Cooper (1986) reported

five features of the visual pathways (characters 4–8 in table 2) that distinguish megachiropterans, dermopterans, and primates from other mammals, including microchiropterans and tree shrews. Using horseradish-peroxidase labeling and electrophysiological recording, they identified these five features in four megachiropteran genera (*Pteropus*, *Rousettus*, *Cynopterus*, and *Syconycteris*) and in the single dermopteran genus *Cynocephalus* and failed to find them in the three microchiropteran genera investigated (the emballonurid *Taphozous*, the megadermatid *Macroderma*, and the vespertilionid *Nyctophilus*). It is unclear how many additional forms from other mammalian orders have been studied to the same level of detail and, therefore, are suitable for outgroup comparison. Pettigrew and Cooper allude to studies on primates, tree shrews, phalangers, and flying squirrels, but provide no specific citations or information regarding taxa and techniques (not surprising, given length constraints on published abstracts).

Our major critique of Pettigrew and Cooper (1986) concerns their characterization of diverse taxonomic groups from study of very few forms. Arguing that these five derived features of the visual system are absent in Microchiroptera from study of three genera seems premature for a group that includes 129 Recent genera. Similarly, their implication that the visual pathways of megachiropterans, dermopterans, and primates are unique among mammals seems unwarranted in light of our rather incomplete knowledge of the patterns among other modern forms.

Smith and Madkour (1980) identified another feature of the central nervous system (character 3 in table 2) that distinguishes mega- and microchiropterans. They noted that microchiropterans, in general, have a relatively small neocortex (although it is enlarged in noctilionids and phyllostomatids); on the other hand, the neocortex is enlarged in megachiropterans, dermopterans, primates, and the tree shrew *Tupaia*. Smith and Madkour (1980: 360) recognized that “volumetric enlargement of the neocortex is not known to be homologous in these cases.” Nonetheless, they used an enlarged neocortex as evidence to ally megachiropterans, der-

mopterans, primates, and scandentians. We are inclined to treat these enlargements as convergences, following the large neuroanatomical literature that has shown that different parts of the neocortex expand in these groups (see Henson, 1970; Campbell, 1980).

(2) *Penis*. Smith and Madkour (1980) identified two features of the erectile tissues of the penis (characters 2 and 9 in table 2) that distinguish mega- and microchiropterans. The first concerns the corpus spongiosum, the erectile tissue around the urethra. In the primitive mammalian condition, as reconstructed by Smith and Madkour (1980), the corpus spongiosum is not well organized as a discrete vascular body and is restricted to the proximal portion of the penis. In contrast, in megachiropterans, dermopterans, and primates, the corpus spongiosum is well organized, highly vascularized, and expanded distally into the glans of the penis. The microchiropterans studied by Smith and Madkour (1980) exhibit variability in the distal extension of the corpus spongiosum. However, in most taxa, the corpus spongiosum “is apparent to some extent in the glans penis, but is never expanded there” (ibid.: 357). The second feature distinguishing mega- and microchiropterans concerns accessory corpus cavernosum tissue. Smith and Madkour (1980) maintained that the occurrence of accessory cavernous tissue is primitive for mammals, because it occurs in monotremes, marsupials, and a range of eutherians, including microchiropterans. Megachiropterans differ in that no accessory cavernous tissue is present, and they share this derived feature with dermopterans, primates (except the indriid *Propithecus*), and tree shrews.

Our criticism of Smith and Madkour (1980) is twofold. First, current knowledge of the diversity of erectile-tissue morphologies among modern mammals is so scanty that a fair evaluation of the phylogenetic significance of the variations is not possible. Although Smith and Madkour studied a large number of bat species (150 unspecified taxa), their outgroup analysis was very meager: seven species of primates, four species of lipotyphlan insectivorans, and one species each of tree shrew (*Tupaia glis*), dermopteran (*Cynocephalus variegatus*), and edentate (*Da-*

sypus novemcinctus). We find problematic, in particular, their characterization of a pattern for tree shrews from *Tupaia*, given current views of relationships within Scandentia (see Luckett, 1980a). Smith and Madkour also included observations from the literature on monotremes, dasyurid marsupials, and rodents in their analysis, yet that still leaves 10 modern eutherian orders for which the morphology of the erectile tissues is unknown (or unreported). Several of these orders have been allied with primates in recently published studies (e.g., Carnivora: Shoshani, 1986; Lagomorpha: Miyamoto and Goodman, 1986), and the distribution of character states in these groups may have direct bearing on Smith and Madkour's analysis.

Our second criticism is that Smith and Madkour fail to explore alternative explanations for the distribution of character states. They treat the appearance of accessory cavernous tissue in the primate *Propithecus* as a reversal to the primitive eutherian condition. Alternatively, the condition in *Propithecus* may represent a primitive retention, requiring that the loss of accessory cavernous tissue in other primates be convergent on the condition in megachiropterans, dermopterans, and tree shrews. An evaluation of these alternatives awaits study of more primates. Because *Propithecus* is the only lemuriform that has been investigated thus far, it is not clear whether its penile morphology is representative of other lemuriforms or unique. With regard to the corpus spongiosum, it seems possible that the appearance of this tissue in the glans of the penis is a derived state shared by mega- and microchiropterans, dermopterans, and primates. It is merely the expansion of this tissue within the glans that distinguishes megachiropterans, dermopterans, and primates from microchiropterans.

(3) *Other*. Two hard-tissue characters used by Smith and Madkour (1980) to ally megachiropterans, dermopterans, and primates are a noninsectivorous dentition and broadened distal radius and lunate bones (characters 10 and 11 in table 2). With regard to the former character, Smith and Madkour considered an insectivorous dentition as primitive and any departures from that type and presumed food habit as derived. We are uncertain precisely

what these authors mean by insectivorous and noninsectivorous dentitions, given their vague character description. Despite a herbivorous diet, modern dermopterans retain relatively primitive tritubercular molars (Rose and Simons, 1977), and the molars of the earliest plesiadapoids (Kay and Cartmill, 1977) and euprimates (Covert, 1986) were adapted for feeding on insects. Characterizing microchiropterans as having a primitive insectivorous dentition is also misleading. The morphotypical molar pattern for this group was probably dilambdodonty, where a distinct W-shaped ectoloph joins the outer cusps of the upper molars. Dilambdodonty is a specialized condition among eutherians that has arisen several times, as suggested by its presence in some soricomorph lipotyphlans, scandentians, and microchiropterans (McDowell, 1958; Van Valen, 1967; Butler, 1972, 1980).

A second hard-tissue character shared by megachiropterans, dermopterans, and primates, according to Smith and Madkour (1980), is the broadening of two elements in the wrist, the distal end of the radius and the lunate carpal bone. While the radius is broadened distally in megachiropterans, dermopterans, and some Recent primates, this condition has been acquired independently within Primates because the radius is only very slightly broadened with respect to the shaft in plesiadapoids (Szalay et al., 1975) and early euprimates (Gregory, 1920). Moreover, a broadened distal radius is not an unusual feature, but is widely distributed among mammals (Weber, 1904; Gregory, 1910). The lunate is relatively small in early euprimates and Recent strepsirhines (Gregory, 1920; Lewis, 1965), suggesting that any broadening of that bone has occurred independently within Primates. A large carpal element articulates with the radius in megachiropterans and dermopterans, as Smith and Madkour reported. However, a similar large element also appears in microchiropterans (Norberg, 1970). In none of these forms is this a single carpal bone; it is a fused scaphoid and lunate, a feature that also occurs in monotremes, pholidotans, and some carnivorans, rodents, scandentians, and lipotyphlans (Weber, 1904; Gregory, 1910; Wyss, 1983).

BAT MONOPHYLY

Like Smith and Madkour (1980), we include mega- and microchiropterans along with dermopterans, tree shrews, and primates within the superorder Archonta (fig. 5). However, we caution that this hypothesis of higher-level relationship is not well substantiated. Support is limited to two unique morphological features of the penis and tarsus (characters 1 and 2 in table 3), and the latter, which concerns the modification of the sustentacular facet of the astragalus, is not found in microchiropterans, where this facet is lost altogether (Novacek and Wyss, 1986). Following Wible and Covert (1987), we tentatively ally euprimates and tree shrews (characters 3–6 in table 3), and although the Paleogene plesiadapoid *Plesiadapis* has the archontan tarsal feature (character 2 in table 3), its relationships to other archontans are not secure. The hypotheses of relationships within Archonta that are best substantiated from the morphological evidence are a monophyletic Chiroptera (characters 15–36 in table 3) and a Chiroptera-Dermoptera clade (characters 7–14 in table 3).

A grouping of chiropterans and dermopterans has been discussed previously by Novacek (1982, 1986; Novacek and Wyss, 1986) and Wyss (1983). We repeat here that the evidence for this clade comes from both cranial and postcranial features. The latter could be viewed as convergent specializations for aerial locomotion, but bats and dermopterans share several similarities of the postcranium not found in other gliding mammals. For one, bats and dermopterans have ulnae that are drastically reduced at both their proximal and distal ends: the olecranon process is weakly developed and the distal ulna tapers to a thin rod that fails to contact any carpals. Also, bats and dermopterans have a muscle of the flight membrane, the humeropatagialis (Leche, 1886; Strickler, 1978), absent in other gliders. (Another flight-membrane muscle shared by bats and dermopterans, the coracocutaneous, also appears in the gliding rodent *Anomalurus* [Parsons, 1899].)

Chiropteran monophyly is supported by the 6 cranial characters discussed in this report and an additional 16 from other anatomical systems, taken largely from previous analyses

by Novacek (1980a, 1982; Novacek and Luckett, unpubl. study) and Luckett (1980b). Many of the latter are features of the postcranium and, therefore, could be viewed as convergent specializations for the acquisition of powered flight. Below we comment on some of these features, including several not so easily connected with flight adaptations.

(1) *Proximal tarsus*. Novacek (1980a, 1982) has identified three derived features in the highly modified proximal tarsus of bats (characters 27–29 in table 3). Typically in mammals, the trochlea of the astragalus has guiding ridges on its medial and lateral borders, which contact the tibia and fibula, respectively. In bats, these ridges are undeveloped and the trochlea itself is poorly differentiated from the astragalar body and neck (particularly in megachiropterans). A second feature concerns the joint between the astragalus and calcaneum, which in therians generally includes a convex astragalocalcaneal facet on the dorsomedial surface of the calcaneum (see Szalay, 1977). In contrast, in megachiropterans, articulation between these bones is achieved via a semilunar depression on the medial surface of the calcaneum (see Novacek, 1980a: fig. 22E), and in microchiropterans, the astragalus is “locked” in position by bony projections on the medial surface of the calcaneum and on the distal astragalar neck. A third feature is the absence in bats of the peroneal tubercle of the calcaneum (beneath which the tendon of the peroneus longus muscle passes). Loss or marked reduction of the peroneal tubercle occurs in a number of modern eutherians including tupaiine scandentians and euprimates (Novacek, 1980a), members of groups thought to be closely related to bats (figs. 4, 5). But the peroneal tubercle is well developed in ptilocercine scandentians and plesiadapids and distinctly present in some Paleogene euprimates (Szalay et al., 1975; Novacek, 1980a), suggesting that this process has been lost independently in bats, tupaiines, and (within) euprimates.

(2) *Flight muscles*. Five unique muscles have been associated with the wings of bats (Vaughan, 1970), but this claim is not entirely valid (a problem reviewed by Wyss, 1983, and personal commun.). Two of these muscles (the coracocutaneous and humeropata-

gialis) appear to have homologs in dermopterans (Leche, 1886). A third muscle, the tensor plagiopatagii, has not been identified in any megachiropteran. The remaining two muscles, the depressor osseous styloformis and occipitopollicalis, apparently are unique to mega- and microchiropterans (characters 30 and 31 in table 3). The depressor osseous styloformis, which thus far has been described for only a few mega- and microchiropterans (Mori, 1960; Vaughan, 1970), runs from the calcaneum to the calcar, the slender cartilaginous or osseous element projecting from the calcaneum into the adjacent border of the uropatagium. The calcar appears in all Recent bats except rhinopomatids, craseonycterids, and some phyllostomatids (Koopman, 1984), where it is presumably secondarily lost. The occipitopollicalis muscle has been described for representatives of all families except Craseonycteridae, Furipteridae, Myzopodidae, and Mystacinidae, for which dissections have not been completed (see Strickler, 1978). It arises from the lambdaoidal crest of the occiput adjacent to the midline, runs in the leading edge of the propatagium, and inserts on the second metacarpal or the base of the pollex (Vaughan, 1970; Strickler, 1978). It has been suggested by Leche (1886) that the chiropteran occipitopollicalis might be homologous with a dorsal slip of the jugalis propatagii of dermopterans, but this homology is unlikely (Wyss, 1983). The dermopteran jugalis propatagii arises from the skin of the cheek and the ventral surface of the zygomatic arch near the external acoustic meatus, and a similarly placed muscle, the facialis propatagialis, has been described along with the occipitopollicalis for the megachiropteran *Pteropus* (Schumacher, 1931; Mori, 1960).

(3) *Forelimb somatosensory representation*. Somatotopic maps, systematic representations of the body surface in somatic sensory areas of the cerebral cortex, have been completed for a few standard laboratory mammals: the marsupial *Didelphis marsupialis*, the carnivorous *Felis catus*, the rodents *Rattus* sp. and *Sciurus carolinensis*, the scandentian *Tupaia glis*, and the primates *Galago crassicaudatus*, *Aotus trivirgatus*, *Saimiri sciureus*, *Cebus capucinus*, and *Macaca fascicularis* (Kaas, 1983). Recently, two bats have

been studied, the megachiropteran *Pteropus poliocephalus* (Calford et al., 1985) and the megadermatid microchiropteran *Macroderma gigas* (Wise et al., 1986). The bats differ from the other mammals in that the somatotopic representation of the forelimb is the reverse of that of the rest of the body (character 36 in table 3), which, according to Calford et al. (1985), reflects the habitual spatial orientation of the bat forelimb (caudal to the head during flight and above it during rest). Minor differences in the somatotopic maps of the two bats (e.g., *Macroderma*, an echolocator, has a greater area devoted to the pinnae than the visually oriented *Pteropus*) have been used by Wise et al. (1986) to support independent evolution of mega- and microchiropterans. However, we view the overall similarity and uniqueness of the bat pattern as further evidence for a single origin for powered flight; minor differences in the maps of mega- and microchiropterans reflect different sensory specializations within the aerial niches (e.g., visual domination versus echolocation).

(4) *Molecules*. Despite the large number of molecular studies in the last few years, only one has treated both mega- and microchiropterans separately and, therefore, is pertinent to our discussion of bat relationships. This was a study of albumin immunological distance data covering a wide assortment of nonungulate eutherians by Cronin and Sarich (1980). These authors reported that, using edentates as a reference group, mega- and microchiropterans share a more recent ancestry with each other than they do with either primates, dermopterans, or the scandentian *Tupaia*. It is not clear how many different bats were sampled for this study; at a minimum, there were several megachiropterans and representative emballonurids, rhinolophoids, mormoopids, phyllostomatids, and vespertilionoids.

CONCLUSIONS

Two radically different hypotheses of chiropteran relationships have been evaluated in the foregoing, each claiming support from the morphological evidence. No matter which hypothesis we choose as the "correct" bat phylogeny, some morphological convergence

occurs. How do we choose which characters are more likely to arise independently?

Pettigrew and Cooper (1986) claimed that convergent evolution of the visual system in megachiropterans, dermopterans, and primates is less likely than independent evolution of flight in bats. We see no a priori reason why the visual system or any other neuroanatomical system is subject to less convergence than other portions of the anatomy. In fact, Pettigrew defeated his claim elsewhere (in Wise et al., 1986) by arguing for the convergent acquisition of the reversed pattern of forelimb somatosensory representation in mega- and microchiropterans. Moreover, other authors (Johnson et al., 1982) have shown that many neuroanatomical traits exhibit significant homoplasy in mammals. Clearly, nervous tissue is more subject to homoplasy than Pettigrew and Cooper acknowledge. Finally, we are not just evaluating convergence in the visual system versus convergence in the flight apparatus; there are characters from other anatomical systems on both sides that need to be weighed.

As stated earlier, the basis for weighting we follow is the distributions of the characters themselves, with emphasis on characters that seem to unite many species in monophyletic groups and repeatedly resist contradiction. Our review has revealed six derived characters (one from the penis and five from the visual pathways) that megachiropterans share with dermopterans and primates but not with the microchiropterans investigated. The distributions of these six characters are not well known either within those taxa or in other mammals. In contrast, there are 22 derived characters (6 from the cranium, 3 from the fetal membranes, and 13 from the postcranium) shared by mega- and microchiropterans that do not occur in dermopterans or primates. The distributions of many (but not all) of these characters are well known among these and other mammalian taxa. Several of the cranial and postcranial characters are unique to mega- and microchiropterans among mammals and most are unusual in their occurrences. In addition, many of the 22 bat characters, including some from the postcranium, are not obviously connected with adaptations to powered flight. Given the distributions of the characters, the most ef-

ficient arrangement of the current morphological data is the cladogram depicting bats as a monophyletic clade (fig. 5).

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