

The evolution of flight and echolocation in bats: another leap in the dark

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ABSTRACT

The earliest known complete bats, from the Eocene (49–53 Mya), were already capable of flapping flight and echolocation. In the absence of direct fossil evidence there have been many speculative scenarios advanced to explain the evolution of these behaviours and their distributions in extant bats. Theories assuming chiropteran monophyly have generally presumed the ancestral pre-bat was nocturnal, arboreal and insectivorous. Following this assumption hypotheses can be divided into the echolocation first, flight first and tandem development hypotheses, all of which assume that flight evolved only once in the lineage. In contrast, the chiropteran diphyly hypothesis suggests that flight evolved twice. Evidence supporting and refuting the different hypotheses are reviewed. It is concluded that there are significant problems attached to all the current models. A novel hypothesis is advanced, which starts from the assumption that bats are monophyletic and the ancestral pre-bat was arboreal, but diurnal and frugivorous. After the evolution of flight it is suggested that these animals were driven into the nocturnal niche by the evolution of raptorial birds, and different groups evolved either specialised nocturnal vision (megachiropterans) or echolocation (microchiropterans). A block on sensory modality transfer has retained this distribution of perceptual capabilities ever since, despite some Megachiroptera evolving rudimentary echolocation, and the dietary convergence of some Microchiroptera with the Megachiroptera. The new hypothesis overcomes many of the problems identified in previous treatments.

Keywords: evolution, flight, echolocation, Chiroptera

INTRODUCTION

The earliest complete fossil bats (Chiroptera) date from the early Eocene (49–53 million years ago). The Eocene bat fauna is extremely rich, comprising hundreds of individual specimens, belonging to 24 genera, including several spectacular forms that are preserved in their entirety (Simmons & Geisler, 1998). Eocene bat fossils have been recovered from Europe (Habersetzer & Storch, 1987, 1989), North America (Jepsen, 1966), Africa (Sige, 1991) and Australia (Hand *et al.*, 1994). The only possible bat remains from prior to the Eocene are a few teeth from the late Palaeocene (Gingerich, 1987), but their chiropteran affinities have been questioned (Hand *et al.*, 1994).

The exceptional preservation of the soft tissues of some specimens of bats from the Messel deposits (49 Mya) confirms that the Eocene bats had wing membranes (Habersetzer & Storch, 1987) and details of articulation of the shoulder and the enlarged scapulae for attachment of flight muscles (Jepsen, 1970) leave no doubt that they were all capable of powered flapping flight (Habersetzer & Storch, 1989; Norberg, 1989). A second important feature of these

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bats is that they have enlarged cochleae relative to the size of the skull (Novacek, 1987, 1991; Habersetzer & Storch, 1989, 1992). Modern bats with enlarged cochleae are all capable of echolocation, while modern bats that do not echolocate, or have reduced reliance on this form of perception, do not show the same extent of enlargement (Henson, 1970). Since Eocene bats have enlarged cochleae, and also modified auditory ossicles comparable with those of extant echolocating bats (Novacek, 1985), they were also clearly capable of echolocation (Novacek, 1985, 1987, 1991; Habersetzer & Storch, 1989, 1992). By 53 Mya, therefore, two major behavioural innovations that we currently associate with bats – flight and echolocation – had already evolved. It is remarkable that in many respects the bats that suddenly appear over the entire globe, in the Eocene are ‘completely developed’ (Habersetzer & Storch, 1989).

The problem presented by the sudden appearance of ‘completely developed’ bats in the fossil record was recognized by Darwin (1859) in the *Origin of Species* (see Chapter 5: Problems with the theory). Darwin (1859) suggested that the bats posed a problem for the theory of evolution because a credible scenario for the evolution of a flying bat from an insectivorous terrestrial mammal, by the process of natural selection, was too difficult to imagine. This point has been used since as an argument in favour of special creation, e.g. Morris (1974). Despite Darwin’s suggestion that constructing a credible scenario was too difficult, there have been many attempts to reconstruct the manner by which the traits evolved, and their subsequent distributions in extant bats. Extant bats are all capable of powered flapping flight, but include non-echolocating as well as echolocating forms, in part mirroring their diverse dietary specialisations. In the absence of direct evidence, however, all the reconstructions are necessarily intellectual ‘leaps in the dark’.

Probably the least credible of these leaps into darkness is the suggestion by Gupta (1984) that bats evolved from pterosaurs. The last pterosaurs disappeared towards the end of the Cretaceous, 12 million years prior to the Eocene. Even if the timing made the evolution of bats from pterosaurs possible, this hypothesis completely ignores the well-established archosaurian diapsid heritage of the pterosaurs (Wellnhofer, 1995), in contrast to the bats, which are very clearly eutherian mammals, derived originally from the synapsid therapsids of the Triassic. Bats did not evolve from pterosaurs. Unfortunately, making such a definite assessment of the other hypotheses is not possible.

Since there are two key behavioural traits, there are at least three scenarios for their evolution: echolocation may have evolved first (Hill & Smith, 1984; Fenton, 1984; Fenton *et al.*, 1995; Arita & Fenton, 1997), flight may have evolved first (Simmons & Geisler, 1998), or the two may have evolved in tandem (Norberg, 1985a,b, 1989; Rayner, 1991a, 1991b; Speakman, 1993; Arita & Fenton, 1997). This minimal view assumes that at least one of the behaviours evolved only once. Multiple origins of both traits (e.g. Pettigrew *et al.*, 1989; Rayner, 1991a) could lead to much more complex interrelationships.

It is useful, before elaborating these different hypotheses, to explore the common ground on which most of the established ideas are based. It is almost universally assumed in models of the evolution of bat flight that the ancestor to the bats was arboreal, and that consequently chiropteran flight evolved ‘from the trees down’. Most treatments also agree that the ‘pre-bats’ shared two other behaviours: they were nocturnal and insectivorous (but see Ferrarezi & Gimenez, 1996). For example, Padian (1987) states ‘*it is clear that the common ancestor (of bats) . . . was small, nocturnal, insectivorous and probably arboreal.*’ The reasons for these assumptions are seldom stated, but appear to be based on the following logic. Almost without exception modern bats are nocturnal (see Speakman, 1995 for some rare exceptions). It is more parsimonious therefore to suggest the ancestors of bats also exhibited this trait. The

role of the hind limbs of bats, in supporting the flight membrane, make an origin for flight from a cursorial ancestor very unlikely (Padian, 1987). Consequently, an arboreal habit seems intuitively much more probable. Finally, the ancestors of all eutherian mammals are generally presumed to have been insectivorous, since these small insectivorous mammals dominate the Jurassic and Cretaceous mammal fossil record. Some modern Insectivora have primitive echolocation systems (e.g. shrews: Gould *et al.*, 1964; Tomasi, 1979; Forsman & Malmquist, 1988), and the potential link of nocturnal insect-eating mammals with primitive echolocation to modern nocturnal insect-eating bats with sophisticated echolocation seems to have been too attractive to resist (Jepsen, 1970; Hill & Smith, 1984; Kovtun, 1989; Thomas, 1998).

In the main part of this review I will summarize the four major hypotheses concerning the evolution of flight and echolocation in bats, and provide evidence which supports and refutes each particular idea. I will follow this analysis with a novel hypothesis, which overcomes some of the difficulties with previous models.

HYPOTHESIS ONE: ECHOLOCATION FIRST

The echolocation-first hypothesis (Fenton, 1984; Hill & Smith, 1984; Fenton *et al.*, 1995; Arita & Fenton, 1997), in common with the other hypotheses, suggests that the original arboreal progenitor of the bats was a small nocturnal insect-eating mammal. This animal probably used ultrasound as a method of communication (Fenton, 1984), very much like some modern Insectivora (citations above) and some other small mammals such as rodents (Sales & Pye, 1974). The hypothesis suggests that in addition to gleaning insects from branches and other surfaces, the animal would reach out from branches and capture insects that were flying past (Jepsen, 1970): called reach-hunting (Speakman, 1999). This would involve some sensory skill in predicting the trajectory of the insects in darkness. The animals may have modified their ultrasound communication calls into broadband biosonar calls to enhance their capabilities to track incoming insects. The calls would have become frequency modulated to maximize the ranging information (Fenton, 1984). The digits of the pre-bat would have been already elongated during the transition to the arboreal habit (Kovtun, 1989). It is hypothesized that the arms and hands of the animal would have become even further extended (Jepsen, 1970), allowing it to reach further outwards to capture passing insects. Over time, the animal would develop a sophisticated echolocation system capable of tracking incoming targets from a stationary position, and enlarged hands with webbing between the digits, capable of capturing the passing insects. The large webbed hands would thus be an exaptation pre-adapting the animals for flight. An alternative explanation for the development of the wing membrane as an exaptation (Kovtun, 1989) was that its primary function was to dissipate heat (Reeder & Cowles, 1951; Cowles, 1947). However, the need for a small nocturnal endotherm to dissipate heat by further enlargement of its surface area is improbable (see also Lancaster *et al.*, 1997), and this idea has not been widely accepted.

Under the reach-hunting scenario, at some point, the animals would start leaping outwards to extend the range over which they could capture passing insects. The animal would track an incoming target, using echolocation from a stationary position, and would then leap outwards towards the insect, using its enlarged hands to capture the prey item. It might then glide, using the large surface area of the hands to aerodynamic advantage, and continue to echolocate in flight to locate a suitable landing site (either on the ground or another perch). From this point onwards the sophistication of the flight would increase to enhance the prospects of capturing the insects, improve mobility in the arboreal habitat and facilitate return to the hunting perch. Eventually, the bats would be feeding in a perch-hunting (or fly-catching) manner – sallying forth from a fixed site to capture passing insects that strayed

within range of the echolocation system (Hill & Smith, 1984). After prey capture the animals would use echolocation to reorient themselves back to the same or another perch.

The next innovations in this process would be to abandon the perch, and start continuous aerial hawking as a feeding strategy. The bats would then be free to pursue flying insects continuously. This would also allow them to exploit landed insects in locations that they could not reach from a terrestrial approach, because their body weight could not be supported by the substrate, for example insects in flowers and on leaves. This would develop in some individuals into a gleaning strategy, and perhaps other foraging behaviours such as nectivory, frugivory (Vogel, in press) and folivory (Kunz & Ingalls, 1994). Once some bats stopped feeding on insects, the needs for sophisticated echolocation might diminish because their 'prey' would no longer be moving in complex three-dimensional spaces, but rather would be stationary and more easily found. Echolocation may have been lost in these animals (Fenton *et al.*, 1995; Hutcheon *et al.*, 1998).

Evidence in support of the echolocation-first hypothesis

The echolocation-first hypothesis is consistent with the homology of the flight apparatus across all extinct and living representatives of the Chiroptera, which has been interpreted as indicating that flight evolved in the bats only once (Simmons & Geisler, 1998). Courts (1997) recently observed stationary megachiropterans (*Pteropus livingstonii* and *P. rodriguensis*) capturing insects that had been attracted to a light in their cage. They did this by extending their wings and scooping the passing insects inwards and then eating them. This behaviour, which was hypothesized to be innate, would be similar to the proposed prey capture behaviour of the earliest pre-bats. These megachiropterans do not echolocate, and their prey capture behaviour is therefore consistent with the absence of sophisticated echolocation in the earliest ancestors.

There are several species of extant bats which forage using perch hunting (e.g. many of the Rhinolophidae: Schnitzler *et al.*, 1985; Neuweiler *et al.*, 1987; Jones & Rayner, 1989). Echolocation is absent in the majority of the Megachiroptera, which are predominantly frugivorous or nectivorous, and independently much reduced in the frugivorous microchiropteran Phyllostomidae (Rayner, 1991a). However there are some echolocating megachiropterans (Griffin *et al.*, 1958; Gould, 1988), which the hypothesis suggests are lineages of bats that lost echolocation but then secondarily regained it, using different mechanisms for sound production (Fenton *et al.*, 1995; Teeling *et al.*, 2000) such as tongue clicking and wing flapping. This interpretation, that the echolocating megachiropterans are recent rather than ancient lineages, is supported by molecular data on the phylogeny of the Megachiroptera (Springer *et al.*, 1997).

Norberg (1989) examined the wing sizes and shapes of the earliest fossil bats and concluded that they had low aspect ratios, and Simmons & Geisler (1998) noted that such low aspect ratios are also found in many modern perch-hunting bats; thus, the wing shapes of the earliest fossil bats (*Icaronycteris* and *Archaeonycteris*) are consistent with perch-hunting preceding aerial hawking. Simmons & Geisler (1998) also noted that *Icaronycteris* and *Archaeonycteris* lack calcars. Since many aerial hawking bats capture insects in their uroptagia, they suggested the absence of the calcar was indicative of perch-hunting in these bats, which thus proceeded aerial hawking as a foraging strategy.

The suggestion that perch-hunting preceded aerial hawking is also consistent with ontogenetic observations in the Little Brown Bat (*Myotis lucifugus*) that juveniles pass through a phase of perch-hunting prior to aerial hawking (Buchler, 1980). Moreover it has been suggested that perch-hunting is probably the ancestral foraging behaviour (Hill & Smith, 1984).

on the grounds that it is more energetically efficient than aerial hawking (Simmons & Geisler, 1998).

Evidence against the echolocation-first hypothesis

Insectivory by reaching outwards and capturing passing prey has never been observed as a foraging strategy in the wild. This is probably because the volume of air that a mammal with even moderately extended arms could sweep through is very small. The energy returns from such a strategy would consequently be minimal, unless insect densities were extraordinarily high. I have calculated the likely energetic returns from a reach-hunting strategy if it was employed by a tree shrew (Tupaiaidae), which is commonly regarded as the nearest terrestrial sister group to the Volitantia (dermopterans and bats). Using such a foraging strategy a tupaiaid would need to feed for more than 24 h each day to obtain its daily energy requirements (Speakman, 1999). While reach-hunting for insects might allow supplementation of the diet, it is unlikely to be a primary feeding behaviour. Although Courts (1997) observed pteropodids performing such behaviours in captivity, the bats did this at a light source, which artificially raised the local insect abundance, possibly making it a profitable strategy. Moreover, the pteropodids performing this behaviour had already evolved massively extended digits, making reaching a more profitable option.

There is a second problem with the energetic profitability of intercepting passing insects by echolocating onto them, and that is the potentially high costs of echolocating when stationary (Speakman *et al.*, 1989; Speakman *et al.*, in press). Stationary bats echolocating at rapid rates and making loud calls may pay very high costs for producing the echolocation calls, and these costs would further depress the profitability of the echolocating and reaching-out strategy for prey capture. The hypothesized 'low costs' of perch hunting for ancient bats and its supposed 'energetic efficiency' are probably therefore erroneous, and in any case beg the question of why aerial hawking would develop at all if it was less efficient. Ontogenetic changes in Little Brown Bat foraging behaviour (Buchler, 1980) are probably closely linked to developmental changes in flight muscle capabilities (Powers *et al.*, 1991) which may be initially inadequate to perform aerial hawking, rather than energetic advantages of perch-hunting.

Although there are currently many examples of perch-hunting bats (Hill & Smith, 1984; Schnitzler *et al.*, 1985; Fenton, 1986, 1990; Fenton *et al.*, 1987, 1993; Neuweiler *et al.*, 1987; Jones & Rayner, 1989), bats that vocalize frequently when they are stationary have a derived skeletal and muscular morphology (Lancaster *et al.*, 1995). These morphological traits (particularly the well-developed abdominal aponeurosis: Kovalena, 1989; Lancaster & Henson, 1995), appear to have evolved to store energy, thereby reducing the costs of stationary echolocation (Speakman *et al.*, in press). Recent measurements of the costs of echolocation in bats with these derived features indicate that the costs of echolocation are indeed lower than in aerial hawking forms, which have less musculo-skeletal specialisation (Speakman *et al.*, in press). These skeletal morphological traits, which include fusion of the ribs to the sternum, vertebrae and each other, are derived and not plesiomorphic, since they are absent in the ancient microchiropterans *Icaronycteris*, *Archaeonycteris*, *Hassionycteris* and *Palaeochiropteryx* (Habersetzer & Storch, 1987). This morphology strongly suggests that aerial hawking as a foraging strategy preceded stationary perch hunting.

The aspect ratios and wing shapes of *Icaronycteris* and *Archaeonycteris*, which Simmons & Geisler (1998) inferred were consistent with perch-hunting, are also typical of bats that must fly in complicated habitats and require high manoeuvrability (Norberg, 1986a, 1986b, 1989; Habersetzer & Storch, 1989). These traits may therefore reflect the arboreal habitat

rather than perch-hunting behaviour. The most extensive reconstruction of flight behaviour in the ancient bats (Habersetzer & Storch, 1989) did not conclude that any of the Eocene bats were perch-hunters but that they were all aerial hawkers. The basis of the argument of Simmons & Geisler (1998), that the absence of a calcar in *Icaronycteris* and *Archaeonycteris* is consistent with perch-hunting, and thus perch-hunting preceded aerial hawking, is unclear. Some groups without calcars (e.g. Rhinopomatidae) are successful aerial hawkers (Schmidt & Joerman, 1983), while many bats which never feed on insects in flight (e.g. megachiropterans) have well developed calcars (Simmons & Geisler, 1998). Presence or absence of the calcar therefore cannot be used to infer whether the earliest known bats were perch-hunters or aerial hawkers.

The cladistic positioning of the megachiropterans indicates a very early divergence from the microchiropterans, which is inconsistent with the suggestion that frugivory and loss of echolocation are derived traits (Padian, 1987; Ferrarezi & Gimenez, 1996). The theory suggests that early megachiropterans lost the ability to echolocate when they started to feed on fruit and nectar. However, microchiropteran frugivores have not lost the capability to echolocate (e.g. Kalko & Condon, 1998), and those megachiropterans that have evolved echolocation are very successful in terms of their widespread distributions compared with the rest of the suborder. This suggests that even in frugivorous bats echolocation provides advantages, and would be unlikely to be lost but then later re-evolve using an alternative sound-generating mechanism (Hill & Smith, 1984; Rayner, 1991a; Speakman, 1993). It seems far more likely that, if echolocation conferred some advantage, it would not be lost in the first place. Moreover, it may have been difficult to swap the dominant sensory modality from a sophisticated echolocation system to a sophisticated nocturnal visual system (see below).

HYPOTHESIS TWO: FLIGHT FIRST

In the flight-first hypothesis the arboreal nocturnal insectivorous mammal is suggested to have first evolved gliding as a progression from leaping between branches of the trees (Smith, 1977; Norberg, 1985b, 1986a; Rayner, 1986; Arita & Fenton, 1997; Simmons & Geisler, 1998). An alternative model in which the pre-bat moved directly from perching to hovering flight (Jepsen, 1970; Pirlot, 1977) is not widely accepted, because hovering flight is the most energetically expensive mode of flying (Clark, 1977; Rayner, 1986; Winter, 1998; Winter *et al.*, 1998). In contrast, gliding is energetically much cheaper (Baudinette & Schmidt Nielsen, 1974). An initial gliding phase would involve extension of the digits and growth of membranes between the digits to enhance the lifting surface (Ledenev, 1989; Smith, 1977). Gliding was gradually replaced by powered flight as this allowed the animals far more flexibility in their locomotion, and provided energetic and other benefits in terms of increased foraging ranges, reduced costs of transport (Schmidt Nielsen, 1972; Rayner, 1986; but see Balda *et al.*, 1985) and reduced predation risk (Pomeroy, 1993; Speakman, 1993). By chance, the evolution of flapping flight may have been facilitated by the positioning of the digits to subdivide the wing membrane (Hill & Smith, 1984). This positioning would allow differential cambering, tensioning and folding of the membrane over its surface, which are essential aspects of flapping a wing, but options that are unavailable in membranes that are not subdivided in this manner, such as those found in some current gliders (e.g. flying squirrels: Thorington, 1984). Once powered flight had developed there might have been some divergence in the foraging behaviour of the animals, with some of them feeding predominantly on insects taken from the substrate and colleagues feeding predominantly on fruit.

The pre-bat animals feeding on insects would have occasionally encountered their insect prey in flight and perhaps eaten them by scooping them into their wings (a reversal of the

capture device being a pre-adaptation to flight: in this case the flight device was pre-adapted to capture insects). For these animals it is suggested that a sophisticated echolocation system evolved, taking advantage of the energy saving (Speakman & Racey, 1991) that is possible by the mechanical coupling of wing beats and echolocation calls (Schnitzler, 1968; Suthers *et al.*, 1972; Lancaster *et al.*, 1995). This would then allow efficient exploitation of aerial insects. Once developed, these bats could chase insects in flight, and aerial hawking would develop as a foraging strategy. Stationary perch-hunting evolved later as a specialised derived behaviour, including the morphological modifications of the abdominal wall (Kovalena, 1989; Lancaster & Henson, 1995) needed to overcome the high costs of stationary echolocation (Speakman *et al.*, 1989; Speakman *et al.*, in press). Once flight had evolved, however, echolocation did not occur early in the ancestry of the frugivorous animals. These bats developed specialised visual systems instead, although two groups later also developed echolocation. Schnitzler (in press) and Simmons & Geisler (1998) both incorporated into their versions of the flight-first theory a phase where perch-hunting precedes full aerial hawking. However, this phase is an unnecessary aspect of the model and arguments against it are presented above.

Evidence in support of the flight-first hypothesis

The flight-first theory is compatible with the morphological evidence from wing structures that flight evolved in the Chiroptera only once. However, it is superior to the echolocation-first hypothesis in several respects. It suggests that aerial hawking is the primitive foraging strategy of the insectivorous bats, and that stationary perch-hunting is a derived state (but see versions of the theory developed by Simmons & Geisler, 1998 and Schnitzler (in press)). This is more consistent with the morphological features connected with energy conservation during echolocation found in modern bats that adopt these two foraging styles. The hypothesis also does not involve a stage of reach-hunting, using echolocation, which is likely to be unprofitable (Speakman, 1999). The theory adequately explains the non-echolocating status of most megachiropterans and the echolocating innovations in this group.

The suggestion that echolocation developed after fully powered flight had evolved is consistent with the suggestion that the coupling of wing beating, respiration and echolocation is a key innovation, because of the energetic efficiency of this combination (Speakman *et al.*, 1989; Speakman & Racey, 1991; Rayner, 1991b; Speakman, 1993; Jones, 1993; Arita & Fenton, 1997). Until bats flapped their wings, they could not benefit from this coupling. Even gliding animals would not benefit from the coupled system. Jones (1993) noted that the coupling of wing beat frequency, respiration and echolocation appears to be very rigid, such that echolocating insectivorous bats hardly ever glide in flight. For example, the Pipistrelle Bat (*Pipistrellus pipistrellus*) glides for only about 13% of its flight time (Thomas *et al.*, 1990; Kalko, 1994), yet a similar-sized bird, the Sand Martin (*Riparia riparia*), glides for up to 79% of the time (Jones, 1993). The lack of gliding behaviour in insectivorous bats is very strong evidence that the coupling of fully functional echolocation to wing beating is an extremely advantageous system. This is because gliding is less expensive than flapping (Baudinette & Schmidt-Nielsen, 1974) and selection would favour its incorporation into flapping flight whenever possible, to reduce total flight costs.

Evidence against the flight-first hypothesis

This hypothesis fails because it makes unrealistic assumptions about the behaviour of the ancestral pre-bats in darkness. It is extremely unlikely that a pre-bat would leap from branches into darkness in the hope it would be able to glide to a landing site (Padian, 1987; Schnitzler, in press). Moreover, lacking morphological modifications to reduce terminal

velocity, such jumps would often be fatal (Balda *et al.*, 1985). These literal 'leaps in the dark' by the pre-bats, leading to the evolution of the flight apparatus, seem very unlikely to have occurred unless they were closely coupled to some form of sensory development, which would allow the animals to detect their landing site BEFORE they leapt off.

Since animals probably do not leap into darkness, for very sound adaptive reasons, the development of flight was probably linked closely either to the development of echolocation (see the tandem hypothesis below) or to enlargement and refinement of the visual system, such as has occurred in other nocturnal leaping animals like gliding squirrels, dermopterans and bush-babies. In this context it is important to note that the visual systems of nocturnal animals are highly derived and specialised, relative to the visual systems of diurnal animals. There are at least six derived features involved in specialised nocturnal vision: increasing the size of the eye, increased size of pupil and cornea to intercept more light, development of reflective 'eyeshine' to reflect light back onto the retina and concentration of rods at the expense of cones. Although nocturnal animals deal with monochrome low-resolution images, while some diurnal animals must process high-quality full-colour images, it is in nocturnal animals that there is considerable enlargement of the visual cortex at the expense of other areas of the brain (Harvey & Krebs, 1990).

On the assumption that bats evolved from nocturnal antecedents, it seems probable that the ancestral pre-bats had some degree of nocturnal vision. However, if they fed by gleaning prey from the substrate, they may not have required long-distance vision, and hence the degree of refinement of the visual system may have been inadequate to allow more than short jumps between branches. As the animals developed nocturnal vision the ability to make longer jumps between branches would become possible. The sophistication of the jumps and leaps would develop hand in hand with the increasing capacity of the visual system – as presumably happened in modern nocturnal leaping groups. By the flight-first model, powered flapping flight would only be possible in a nocturnal animal that had already committed itself to specialist nocturnal vision, enabling it to detect suitable landing sites. At this stage, however, the visual system was probably inadequate to detect insect prey and intercept it in flight (Simmons & Geisler, 1998)

Animals, however, have only limited cranial capacity. It is not possible to be a sensory master of all modalities because this would require massive enlargement of all the sensory brain areas simultaneously. Animals are generally sensory specialists, with one modality expanded at the expense of the other modes (Harvey & Krebs, 1990; Cooper *et al.*, 1993; Martin, 1981). I have suggested elsewhere (Speakman, 1993) that this selective allocation of brain processing capacity may place animals which are sensory generalists at a selective disadvantage in certain conditions – a nocturnal sensory specialist would be superior at night to a less specialised visually orientated animal. The requirement to specialise results in modern bats relying principally either on echolocation or on vision to orientate, but not on both in equal measure. Although some microchiropterans have well developed visual (e.g. Bell & Fenton, 1986; Joerman *et al.*, 1988) and olfactory capabilities (Thies *et al.*, 1998), they are predominantly echolocators (Kalko & Condon, 1998) with massively enlarged auditory cortex areas in the brain (Metzner, 1991). In contrast, even the echolocating megachiropterans are still predominantly visually orientated (Neuweiler, 1984; Pettigrew *et al.*, 1989). Simmons & Geisler (1998) suggest that swapping modalities would not have been disadvantageous to early bats, because there would be no competitors in the echolocating niche. However, competition is not the argument against swapping modality (Speakman, 1993). It does not matter that an adaptive peak in the landscape is unoccupied if an animal has to pass through an adaptive trough to reach it. The animals are not competing with animals

already in the destination niche, but with versions of themselves in the source niche that do not reduce visual capacity.

Simmons & Geisler (1998) envisaged several advantages that a sensory generalist would have over an animal that remained a visual specialist – such as improved obstacle avoidance when flying and the ability to exploit caves as habitat. These advantages supposedly explain how microchiropteran echolocators could evolve from a visually specialised ancestor. Yet a suite of such advantages raises another unresolved question of how the visually specialised animals were able to still compete and ultimately become the Megachiroptera.

Simmons & Geisler (1998) have suggested that regression of the visual system in early bats has many parallels; for example, the loss of vision in moles (Johnson, 1954; Lund & Lund, 1965, 1966), mole-rats (Cooper *et al.*, 1993) and cave-living fish (Wilkins, 1971; Jeffery & Martasian, 1998). In all these examples, however, the situation is different. These animals inhabit niches where the existence of vision is superfluous, because the animals permanently occupy a fossorial or cavernicolous habitat, where there is absolutely no light. The ancestral types of these animals, with advanced visual systems, were therefore devoting energy and processing capacity to a completely redundant part of the brain. Vision in these animals regressed because it was selectively advantageous to lose it.

The situation being postulated in the flight-first hypothesis is different. Here it is suggested that the animals evolved an extremely specialised and advantageous nocturnal visual system, which then regressed to allow development of another highly derived and advantageous echolocation system. My argument (Speakman, 1993) against this hypothesis was that intermediate animals that had regressed vision, but not yet fully developed echolocation, would have no selective advantage relative to the visual specialist and therefore could not evolve by natural selection. Although the echolocating megachiropteran (*Rousettus aegyptiacus*) lacks the retino-tectal mapping found in other megachiropterans (Thiele *et al.*, 1992), this reorganization is not necessarily visually inferior, and does not conflict with the hypothetical block on modality swapping.

HYPOTHESIS THREE: TANDEM DEVELOPMENT

An alternative to the flight-first hypothesis – where the leaping animal develops flight in tandem with a sophisticated visual system, which is then swapped for a sophisticated echolocation system – is the suggestion that the animals developed an increasingly sophisticated echolocation system in tandem with flight. This idea was suggested by Norberg (1985b, 1989) who proposed that the ancestral animals were small, nocturnal and insectivorous, and used ultrasound to communicate (as in hypothesis number one). These communication calls may have acted as a rudimentary biosonar allowing the arboreal animals to make short leaps in darkness between branches (see also Schnitzler, in press). The length of leaps, glides and ultimately flapping flight would have evolved in this system in parallel with the increasing power and frequency of echolocation pulse production. This would take full advantage of the energetic efficiency of coupling biosonar production to wing flapping (Speakman & Racey, 1991; Rayner, 1991b; Speakman, 1993; Jones, 1993). The loudest and most costly calls would only be required when the animals were able to produce them most efficiently. Initially, the animals would be unable to use the echolocation to capture insects (Norberg, 1989; Schnitzler, in press), but as their echolocation and flight capabilities developed, the animals would evolve aerial hawking.

Once echolocation had evolved in a flapping flying animal, the modern distribution of echolocation systems is explained by the same processes elaborated under the echolocation first hypothesis: megachiropterans lost the echolocation capacity to vision, but rudimentary

forms of echolocation based on tongue clicking and wing clapping re-evolved in this group at a later stage (Griffin *et al.*, 1958; Sales & Pye, 1974; Gould, 1988). Perch-hunting is suggested to be a derived state.

Evidence in support of the tandem-development hypothesis

This hypothesis overcomes the problem of the flight-first hypothesis that an animal would not leap into darkness in the hope of encountering a suitable landing site. It is consistent with the suggestion that flight in the bats has evolved only once, and with full power echolocation developing in tandem with flapping flight to capitalize on the metabolic efficiency of the coupled system.

Evidence against the tandem-development hypothesis

The major drawback of this version of the tandem-development theory is the suggested loss of echolocation capability in early megachiropterans, followed by its secondary evolution using a different mechanism at a later time. Arguments against this idea have been presented above. Moreover, the model also assumes that the primary sensory modality swapped from echolocation to visual, which is presumably as difficult a change to make as the reverse (see discussion above).

An alternative version of the tandem-development idea assumed that the progenitor animal was a non-echolocating (but ultrasound-using) small insectivore (Speakman, 1993). Some of these animals evolved flight by the leaping-gliding-flying route by simultaneous specialisation of the visual system (ultimately becoming the Megachiroptera) while others developed flight by simultaneous development of echolocation (ultimately becoming the Microchiroptera). Rudimentary echolocation systems then emerged much later in some of the megachiropterans. This alternative version has two major advantages over the version detailed above (Norberg, 1985b, 1989; Simmons & Geisler, 1998). First, it obviates the need to explain the loss and re-evolution of echolocation in the Megachiroptera; and second, it avoids any need to invoke swapping of specialised sensory modalities.

The major problem with this alternative version of the tandem-development hypothesis is the assumption that flight developed twice in the lineage. Simmons & Geisler (1998) rejected this suggestion because it would require the parallel development of at least 12 highly derived morphological traits in the postcranial musculoskeletal and nervous systems of mega- and microchiropterans. This level of similarity is highly unlikely to be a result of convergence. However, U.M. Norberg (pers. comm.) has argued that once the evolutionary decision 'has been made' to base the lifting surface on an extension of all the digits of the fingers and the arm, there are limited options available for the structure of many of the flight adaptations. Consequently, what appear to be 12 independent traits may in fact be fewer, since some are inevitable design consequences of others. Moreover, some features that appear in the wings are probably unrelated to flight, but may reflect the shared ancestry prior to development of flight. In addition, the wing morphologies of mega- and microchiropterans are not so similar as they might first appear, and there are significant differences between the two groups (elaborated extensively in the context of the chiropteran diphyly hypothesis by, e.g. Pettigrew *et al.*, 1989).

HYPOTHESIS FOUR: CHIROPTERAN DIPHYLY

The association of bats and primates stretches back to Linnaeus who originally classed bats within the order primates. Subsequently, the bats were classed in their own order (Chiroptera) and included with the primates and several minor groups (tree shrews Scandentia and flying

lemurs Dermoptera) in the super-order Archonta (Simpson, 1945; Van Valen, 1979; Novacek, 1994; Allard *et al.*, 1992). The close interrelationships of bats, primates, tree shrews and flying lemurs has not been in doubt until very recently. The general consensus throughout the majority of the 20th century has been that bats are monophyletic, with mega- and microchiropterans more closely related to each other than to any other group. However, Smith (1976, 1977) suggested that the shared morphometric features between mega- and microchiropterans were not synapomorphic but plesiomorphic and thus concluded that the groups had independent origins. Developing this hypothesis, Smith & Madkour (1980) noted that the megachiropterans shared morphological characteristics of the penis with primates that were not shared by Microchiroptera. This supported the earlier suggestion (Smith, 1976, 1977) that bats are diphyletic, with the megachiropterans derived from the primates, and the microchiropterans derived from another, possibly insectivoran, ancestry.

The idea that bats might be diphyletic did not receive much attention until 1986. In that year Pettigrew (1986a) showed that megachiropterans shared with primates not only penile characteristics but also retino-tectal pathways from eye to cortex, which previously had been considered a diagnostic feature of the primates. Pettigrew (1986a, 1986b) strongly advocated the diphyletic origins of the bats. Evidence supporting this viewpoint accumulated over the next few years, culminating in a major review in which 58 different pieces of morphological data were presented that placed the megachiropterans apart from the microchiropterans and, more importantly, close to the primates (Pettigrew *et al.*, 1989). The brain pathway characteristics, in particular, were considered very unlikely to have convergently evolved, and were also likely to be highly conserved given the embryonic structural reorganization that would be necessary to alter them. At this time, the only data that appeared to favour the monophyletic origins of bats were the structures of the wings, which Pettigrew and colleagues suggested were convergent.

The diphyly hypothesis for the origins of flight and echolocation therefore suggested that microchiropterans evolved from an insectivoran ancestor in the late Cretaceous that had rudimentary echolocation capability (Pettigrew, 1986b). Flight and echolocation in this group are presumed to have evolved by one of the models presented above (i.e. flight first, echolocation first or in tandem). Many millions of years later, probably around the Oligocene, an early primate group began gliding (ultimately becoming a line which led to the dermopterans) and some of these evolved powered flight and became the megachiropterans. Even later than this, some of these bats independently developed novel forms of echolocation (e.g. Gould, 1988). The theory is unequivocal in its suggestion that flight evolved twice and the wing structures of Mega- and Microchiroptera are convergent.

Support for the diphyly hypothesis probably reached its zenith at the 1989 International Bat Research Conference in Sydney, Australia. At that meeting, a packed debate on bat origins appeared to be almost overwhelmingly in support of the diphyletic origins of bats. The only conflicting data presented at that meeting came from Bennett, who had published some molecular work a year previously (Bennett *et al.*, 1988) which involved sequences of the mitochondrial genomes (CO III gene) extracted from *Drosophila*, mouse, cow, megachiropteran and human. The derived trees with greatest probability did not appear to closely link the megachiropteran with the human, as would be anticipated from the diphyly hypothesis. However, the most likely tree also linked cow and human more closely than mouse and human, which was an unexpected result, and there were no data included for microchiropterans. General opinion at the debate was that once better molecular data were available, the issue would be resolved in favour of the diphyly hypothesis.

Better molecular data were not late in arriving, but they did not resolve the issue in favour

of diphyly. By 1992, six molecular papers had been published, and they unanimously supported the monophyletic origins of bats (Adkins & Honeycutt, 1991; Mindell *et al.*, 1991; Ammerman & Hillis, 1992; Baker *et al.*, 1991a; Bailey *et al.*, 1992; Stanhope *et al.*, 1992). In addition, several papers also presented morphological data supporting the monophyly hypothesis. A series of papers in *Systematic Biology* (Pettigrew, 1991a,b; Baker *et al.*, 1991b; Simmons *et al.*, 1991) presented and reviewed much of the conflicting information. By 1995 most feeling had returned to support of monophyletic origins for the bats, principally because of the molecular data. Moreover, the extreme conservation of the brain pathways, which had formed a major aspect of the original diphyly hypothesis, was questioned by observations that the echolocating megachiropteran *Rousettus aegyptiacus* does not have the advanced 'primate' pathway (Thiele *et al.*, 1992). Furthermore, the monophyletic linkage of Mega- and Microchiroptera is founded in extensive morphological as well as molecular evidence (Wible & Novacek, 1988; Greenwald, 1990; Simmons, 1995, 1998). Pettigrew (1995) has presented some convincing evidence that at least some of the molecular work supporting monophyly (e.g. Bailey *et al.*, 1992) is flawed because of arbitrary insertions into the sequences to get them to align. In addition, he presented a working hypothesis why molecular studies might be predisposed to favour monophyly; because of the Arginine–Thiamine (AT) base compositional bias shared by the two groups, which might be dependent on their shared (convergent) use of flight and its high energy demands. However, recent analyses that correct for this bias have failed to produce evidence favouring diphyly (Pettigrew & Kirsch, 1998; Kirsch & Pettigrew, 1998; Hutcheon *et al.*, 1998). Consequently, support for monophyletic origins of bats is still considerably greater than for diphyly.

However, even if one accepts that bats are monophyletic, the morphological evidence linking megachiropterans with the primates remains to be explained, and if convergence of the wing structures of mega- and microchiropterans seems unbelievable, it is scarcely less so than the proposed convergence of brain structures between megachiropterans and primates. The positioning of the Dermoptera also poses several outstanding problems: a close link to primates is well supported by the DNA data, though a link to megachiropterans is not (reviewed in Simmons, 1995), yet morphometric data strongly suggest Dermoptera and Megachiroptera are sister taxa (Novacek, 1987).

Although molecular data have clearly indicated chiropteran monophyly, there has also been a suggestion in some recent papers that the suborder Microchiroptera is paraphyletic. In particular, several analyses have indicated that the Rhinolophidae is more closely linked to the megachiropterans than the microchiropterans (Stanhope *et al.*, 1996; Hutcheon *et al.*, 1998; Teeling *et al.*, 2000). This association is not supported by more comprehensive phylogenies that draw together large character arrays of both molecular and non-molecular evidence (Simmons, 1998; Simmons & Geisler, 1998). Nevertheless, if this association were correct it would have several important ramifications for the models of flight and echolocation developed above. In particular, this linkage may provide some support for the notion that all megachiropterans were originally echolocating animals, some of which lost the capability and developed a convergent visual system with the primates (Teeling *et al.*, 2000). Alternatively, it may indicate that echolocation has more multiple origins than we currently imagine. There are several differences between the echolocation systems of Rhinolophidae and other microchiropterans, which might support this opinion.

ANOTHER LEAP IN THE DARK: A NEW HYPOTHESIS

In developing this hypothesis I have tried to take a new look at the problem, abandoning some of the common assumptions that have underpinned the previous ideas to overcome the

problem areas of the previous explanations. The proliferation of angiosperms in the Cretaceous would have provided large amounts of fruit for exploitation by small mammals (Collinson *et al.*, 1993). Imagine therefore that the ancestral 'pre-bat' was in fact arboreal, diurnal and frugivorous rather than arboreal, nocturnal and insectivorous. Frugivory as the ancestral state in bats is supported by the cladistic analysis of dietary character traits by Ferrarezi & Gimenez (1996). Imagine the arboreal animal leaping from branch to branch using its diurnal visual system to guide it safely to a landing spot, like extant tree squirrels (Sciuridae). Because the animal is diurnal I am assuming that the visual system is not derived, enlarged and as specialised as it would be in a nocturnal mammal. These animals would evolve from leaping to gliding, and ultimately to powered flight. Evolution of flying was presumably driven by the energetic and perhaps anti-predation advantages associated with flight. It would still be frugivorous, visually orientated (but not visually specialised) and able to fly between trees or even over longer distances.

Since these hypothetical animals fed on fruit they would have consistently faced problems meeting a nitrogen balance (Thomas, 1984; Courts, 1998). It would always be advantageous for them to take the occasional insects they encountered to supplement their protein requirements. In flight, the bats would encounter many insects. Capturing these insects by visual orientation would be feasible, and some of the bats might gradually switch from being frugivorous and taking occasional insects to being entirely insectivorous. Two things make insectivory very likely to be an advantageous foraging strategy. First, in the Cretaceous and early Palaeocene there were no aerial insectivorous birds that might compete for the aerial insect resource (Rydell & Speakman, 1995). Recent summaries of early avian evolution have concluded that birds diversified enormously in the Cretaceous following their origin in the mid to late Jurassic (Chiappe, 1995; Hou *et al.*, 1996). The major groups (Enantiornithines and Ornithurines), however, were almost completely eliminated during the later phase of the Cretaceous (Feduccia, 1995, 1996; Chiappe, 1995) leaving only a small group of 'transitional shorebirds' in the early Palaeocene (Feduccia, 1995). Thus, with no avian (or pterosaur) competition, foraging on aerial insects would be a vacant niche (Neuweiler, 1984). [Note that although pterosaurs were around until the end of the Cretaceous most forms after the Jurassic were large fish eaters]. Second, measurements of aerial insect abundance at present suggest insects are far more abundant in late afternoon than they are at night (Speakman, 1995; Rydell *et al.*, 1996) which would be the time when our hypothetical predator would be flying. This raises another problem with the previous scenarios. Given this probable distribution of resource, the previous hypotheses need to explain why the bats did not expand into the vacant diurnal insectivore niche where prey were probably most abundant.

This hypothesis is consistent with the single evolution of flight in the bats and the synapomorphies of the flight apparatus evident in mega- and microchiropterans. It overcomes the problem of 'leaping in the dark' which besets the flight-first hypothesis. It also overcomes the requirement for a non-echolocating nocturnal flying animal to have a specialised and enlarged visual system. During the Palaeocene there was a diversifying group of diurnally active volant mammals, some of which were specialising on fruit and nectar while others were specialising on insects. All the animals were visually orientated but not visually specialised. However, something happened to change this situation. During the Tertiary, bird diversification resumed from the bottleneck it had passed through at the Cretaceous–Tertiary boundary. Over the first 10 million years of the Palaeocene all the modern orders of non-passerine birds had their origins. This includes the diurnal predatory hawks and falcons (Feduccia, 1995). Modern bats are almost exclusively nocturnal, arguably because of the risks of diurnal predation from raptorial birds (Baker, 1962; Neuweiler, 1984; Speakman, 1990, 1991a, 1991b,

1995; Fenton *et al.*, 1994; Fenton, 1995; Thomson *et al.*, 1998 but see Speakman *et al.*, 2000). The evolution of these birds in the Palaeocene would have exerted tremendous predation pressures on the diverse diurnal bat fauna, driving them towards the nocturnal niche. However, animals with capabilities to fly in daylight have insufficient visual capacity to fly and orientate at night (Fox *et al.*, 1976; Kacelnik, 1979). The invasion of the nocturnal niche therefore was only feasible with the development of sensory adaptations to allow the animals to do so. Several strategies evolved, which included enlargement of the eyes and visual cortex (megachiropterans) and the development of echolocation (microchiropterans). The fact that the insectivorous bats became echolocators while frugivores initially orientated visually may have been largely chance (or related to size and wing beat frequency in larger frugivorous bats: Jones, 1994, and perhaps the inability of the eyes of small animals to become nocturnally specialised: Scholey, 1986). However, once the systems developed, sensory specialisation may have precluded wholesale switching of systems, leading to a large degree of phylogenetic inertia. All microchiropterans echolocate – independent of their diverse diets, which include many components shared with megachiropterans such as fruit and nectar – and almost all megachiropterans do not.

This hypothesis is consistent with much of the current information. It is consistent with the evolution of flight once, combined with the current distribution of echolocation systems. It also overcomes the potential problems of swapping specialisations. The biggest problem with the novel hypothesis (and the other theories elaborated above) is how to explain the extensive similarities between the megachiropterans and the primates. A logical possibility is that, rather than the megachiropterans arising from primates, the terrestrial primates arose instead from the flying bats (the ‘fallen angel’ hypothesis: Pettigrew *et al.*, 1989). However, there are no data to support this idea, and a wealth of (molecular) data indicates clearly that primates are not the closest sister group to the megachiropterans. Even when it was first presented (Pettigrew *et al.*, 1989), it was only included as a logical possibility. The most likely scenario is that most of the traits are ancestral to the common archontan ancestor of the primates, dermopterans, tree shrews and bats (Greenwald, 1990), and such features have been progressively lost in the microchiropteran clade but not the megachiropterans (Baker *et al.*, 1991b).

Testing the novel hypothesis

Like most evolutionary reconstructions, a criticism of the novel hypothesis is that it is not a testable proposition but merely a ‘just-so’ explanation for the current trait distributions observed in the bats and related groups. This criticism can also be levelled at the other hypotheses, and the major strength of the novel hypothesis presented here is that it overcomes the most serious criticisms that beset these earlier explanations without raising further problems that are insurmountable. Nevertheless, it would be useful to have ‘tests’ by which the novel hypothesis might be refuted. The following is a non-exhaustive list of three potential ways in which the hypothesis might be refuted.

1. If a fossil bat was found from prior to the Eocene with Megachiropteran affinities but clear evidence that it used echolocation. Alternatively, the hypothesis would be strongly reinforced if a pre-Eocene fossil bat was found with indications that it had diurnal attributes, e.g. no echolocation capacity and diurnal sized eyes (orbits).
2. If current opinion over the evolution of raptorial birds was shown to be erroneous and raptorial birds were common throughout the late Cretaceous and early Tertiary.
3. If insect flight times in the early Tertiary were shown not to peak in daytime.

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