John D. Altringham

SECOND
EDITION

BATS

From Evolution to Conservation

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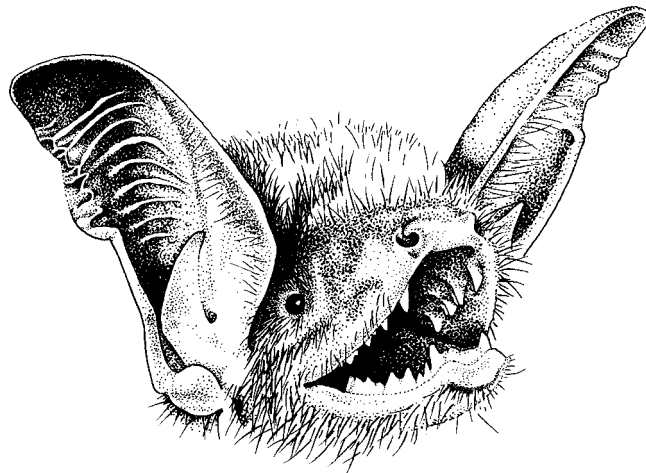
Bats

From Evolution to Conservation

Second Edition

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DRAWINGS BY

Tom McOwat and Lucy Hammond

Myotis myotis (drawing by Lucy Hammond)

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Preface

Preface to the first edition

This book is aimed primarily at undergraduate and graduate students wishing to learn about bats, but also aims to show how a study of one group of animals can contribute to a wider understanding of the processes that shape the natural world. It therefore has two main objectives. The first is to give an account of the biology of the world's bats, emphasizing those aspects are unique or highly adapted, notably flight and echolocation. The second objective is to illustrate processes and concepts of broad biological relevance, many of which are major themes in current research. The coverage is broad, but by no means comprehensive. I have tried to make the book accessible to the growing number of bat enthusiasts in all walks of life, by giving some relevant background to what I imagine are the more difficult sections and by explaining terminology and principles that may be unfamiliar.

Preface to the second edition

In this updated and expanded version my aim has not changed, but the state of bat biology has! Scientific and public interest in bats has grown considerably in recent years and the scientific literature on bats has exploded. There have been significant advances in almost all areas of bat biology and most chapters have required a major rewrite and expansion. In some areas developments have been so significant I have created new chapters. I have also included a major chapter on conservation. My interest in bats began in conservation and it has also been responsible for the shift in my own research from biomechanics to bat ecology. Bats are under threat from habitat destruction, degradation and fragmentation, from climate change, and from the many other pressures humans bring to bear on the planet. They therefore need our help. As a large, diverse, and widespread group of animals, their value as indicators of environmental health has long been evident to biologists and has recently been more widely recognized. Although the book is broader in its scope than its parent it is now even more difficult to be comprehensive, so I apologize if your favourite subject gets too little attention! It is increasingly difficult to do justice to the technical complexity of many areas of study in a book of such breadth. I have tried to walk that fine line: giving you sufficient detail to properly inform without getting you mired in the detail. In bringing you up to date with the key advances in our knowledge and understanding of bats, I hope I have also illustrated some of the major changes in the way we think about and study the natural world.

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Introduction—a biology lesson from the bats

Bats are one of the most successful mammalian orders, and probably the most diverse. The 1,110-plus species provide an unparalleled exhibition of variations on the mammalian theme, and a broad lesson in biology. In the bats we see excellent illustrations of adaptive radiation, optimal foraging, coevolution, convergent evolution, reciprocal altruism, the arms race between predator and prey, the complex interactions between behaviour and population structure and key macroecological and biogeographical principles, to name just a few examples. This is a book about bats, but it will also use them as a vehicle to show how the natural world is shaped.

Rodents are the only mammalian order to outnumber bats with, the last time I looked, 2,227 species, but they are arguably less diverse in their biology. Over 20 per cent of all mammals are bats—surprising when you think that there are about (yes, there's still uncertainty) 29 mammalian orders, including animals as varied as primates, carnivores, cetaceans, rodents, insectivores, ungulates, seals, sloths, and marsupials. Bats are distributed all around the world: over 200 species are found in Africa and Madagascar, over 300 in South and Central America and the Caribbean, and a similar number in South East Asia and Australasia. They are also well represented in higher latitudes: about 40 species are resident in both North America and western and central Europe. Several vespertilionid bats (for example *Eptesicus*, *Lasiurus*, and *Myotis* species) spend the summer north of the Arctic Circle. Other members of this very large family (for example *Dasypterus* species) forage in the chill and windy regions of southern Patagonia. Bats have found their way to most islands, however remote, where they may be the only native
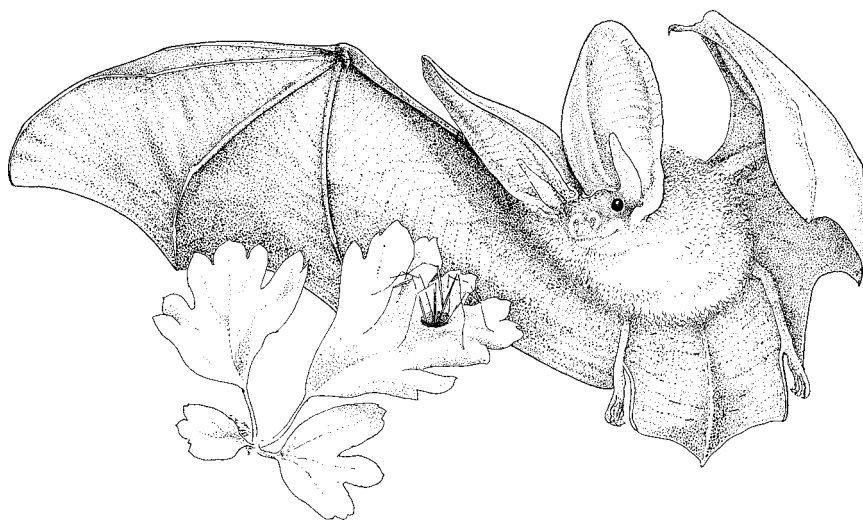
Brown long-eared bat, *Plecotus auritus*

mammals. New Zealand has only two species of land mammal, both bats: one species from the endemic family Mystacinidae, and a vespertilionid. The nearest relatives of *Mystacina tuberculata* are the fisherman bats (*Noctilio*) of South America—one of several possible examples of related families separated by the breaking up of Gondwanaland in the late Cretaceous. This is one of several bits of circumstantial evidence for the very early origin of bats, now supported by firmer evidence from genetic studies. Bats probably witnessed the demise of the dinosaurs in the mass extinction at the end of the Cretaceous.

Bats range in size from one of the smallest mammals (the bumblebee bat, *Craseonycteris thonglongyai*, 1.5–2 g) to 1 kg flying foxes (*Pteropus* species) with wingspans of over 1.5 m. They also come in a wide range of shapes and colours. Most bats are admittedly rather drab, but there are exceptions, like the painted bats (*Kerivoula*), whose bright and cryptic patterning may camouflage them in their exposed tree roosts—some look like flowers and fruit. The tube-nosed fruit bat (*Nyctimene major*) has wing patterning to match the tree trunks to which it clings. The wonderfully grotesque hammer-headed bat (*Hypsignathus monstrosus*) has a nose of immense proportions. Males hang in the trees along rivers and call to passing females, who select the best (the most impressive callers?) for mating. This is one of the best documented examples of lekking in mammals, but more are now being found among bats. Then there's the striking crested free-tailed bat (*Chaerephon chapini*) which distributes pheromones from the erectile crest of hair on its head. The nose-leaves and varied facial protuberances of many bat families are often useful identification features. Most have a functional role in echolocation, for example those of the horseshoe bats (Rhinolophidae), but the function of others has yet to be determined, if indeed they have one!

A complex and exciting story has unfolded around the very origins of bats. Until recently two sub-orders were described, the Megachiroptera, the Old World fruit bats or flying foxes, and the more widespread, more numerous and more diverse Microchiroptera. The traditional and widely-accepted view was that these two sub-orders arose from a common ancestor. However, a substantial and broad-based body of evidence for independent origin, with subsequent convergent evolution, was published during the 1980s. The traditional viewpoint seemed to be shaking on its apparently weak, and largely anatomical, foundations and controversy raged. But new evidence for the common origin of bats emerged from the labs of molecular biologists and anatomists. In the end, the evidence for a common ancestor became overwhelming and the controversy died, but not without generating some fascinating results. In resolving the debate, new and surprising discoveries have been made about the evolution of bats and the origins of flight and echolocation. Ironically and surprisingly (to me at least), the closest relatives to the non-echolocating, Old World fruit bats appear to be the horseshoe bats—the most advanced and sophisticated echolocators!

The niche that many bats exploit as aerial, nocturnal hunters is a demanding one. Flight places major anatomical and physiological restrictions on bats, but the rewards, evident in their success, are great. A better understanding of the aerodynamics of flapping flight stimulated studies of the relationship between wing morphology, flight characteristics, and feeding ecology. Add to flight the ability to locate and catch prey in the dark using sound, and you have in bats a highly adapted product of evolution, with many interesting biological stories to tell. We are only just beginning to understand the complexity, subtlety, and remarkable perceptual abilities of bat echolocation. Advances in technology and some ingenious experimentation have uncovered dazzling feats—such as the ability of greater horseshoe bats (*Rhinolophus ferrumequinum*), at least under laboratory conditions, to distinguish different prey species from the modulated echoes returned by flying insects. Like flight characteristics, the type of echolocation used is determined by environment, foraging style, and the prey sought. Studies of bats in the wild have shown how whiskered bats, *Myotis mystacinus*, subtly alter the structure of their echolocation calls in flight to compensate for errors in target ranging due to Doppler shift and changing position—mechanisms worthy of the most sophisticated modern military technology.

The success of bats in high latitudes is due in no small measure to their ability to reduce body temperature and save energy when insect availability is

low. Torpor is the ability to reset body temperature to a level well below that required for normal activity, to actively regulate it within narrow limits, and to actively return to full operating temperature: few mammals perform this task as well as bats. We commonly think of torpor in the context of the long winter hibernation, but its use is an important part of a flexible, day to day, energy-saving strategy among many temperate bats.

Few potential roost sites have been overlooked by bats. Brazilian free-tailed bats (*Tadarida brasiliensis*) in Central America and the southern United States form cave dwelling colonies that number millions of individuals. The hoary bat (*Lasiurus cinereus*) is a solitary tree dweller, hanging (with its young) from high branches in the boreal forests. Incidentally, this species ranges all the way to South America, and is the only species found in Hawaii. A few species live in underground burrows, and in the case of the African slit-faced bats (*Nycteris* species), those of the aardvark! The short-tailed bat (*Mystacina tuberculata*) of New Zealand frequently forages on the ground, and burrows into fallen and decaying kauri trees, where they roost like peas in a pod. Adaptations for this unusual way of life include tough wings that can be tucked away in pouches on the body, and strong talons on the thumb and toes. Several species (for example *Artibeus*, *Ectophylla*, and *Uroderma*) bite through the main supporting ribs of palm and *Heliconia* leaves to collapse them into tents and, in Gabon, *Myotis bocagei* roosts inside the flowers of the water arum. *Tylonycteris* bats roost inside bamboo shoots, gaining entry through the internodal emergence holes of a chrysomelid beetle. They have fleshy pads or 'suckers' on their wrists and ankles to grip the inside of the culm. Suckers are also present on bats of two other families that roost in furled leaves, the *Myzopoda* of Madagascar and the *Thyroptera* of Central and South America—a good example of convergent evolution.

Bats feed on a wider variety of food than any other mammalian order. Most feed on insects and other arthropods—the Pallid bat (*Antrozous pallidus*) of the south-western United States, and some African slit-faced bats, have a liking for scorpions! One population of the fisherman bat (*Noctilio leporinus*) eats lots of fiddler crabs. Others feed on fish, amphibians, reptiles, birds, mammals (including other bats), fruit, nectar, pollen, occasional leaves and seeds, and of course blood. Many are highly specialized in their diets, but others, including many spear-nosed bats (Phyllostomidae) of South and Central America, are omnivorous and will take insects, vertebrates, and fruit. The very diverse feeding ecologies of bats have been sources for many interesting and informative investigations. The neotropical vine *Mucuna holtonii* bears a modified petal or vexillum that acts as a powerful acoustic mirror, reflecting most of a bat's echolocation call back towards the bat over a wide range of angles of incidence. Wild bats show a very strong preference for flowers with an intact vexillum since it indicates a rich nectar source. Bats don't only use echolocation to find food—passive sound, smell, vision, and even heat sensors are also important. Many bat-pollinated flowers are violet and reflect ultra-violet light, and some bats can perceive this. The nectar-feeding *Glossophaga soricina* was found to be sensitive to wavelengths down to 310 nm, well into the UV. But it does not end there. Even more recently it has been shown that *G. soricina* and *Carollia perspicillata* have cone cells for colour vision, with two types of light-sensitive opsin protein for short (blue/UV) and long (green/red) wavelengths—these bats have all that is necessary for daylight vision, dichromatic colour vision, and UV vision!

Nectar and fruit eating bats also provide the biologist with fascinating examples of coevolution. The long tongues of nectar-feeding glossophagine bats are well known. The record is held by the recently discovered *Anoura fistulata* at 85 mm, 150 per cent of its body length—second only to chameleons within the vertebrates. When not in use, this remarkable tongue is retracted into the thoracic cavity with its base between the heart and the sternum, a structure similar to that independently evolved by ant-eating pangolins. This enormous tongue enables the bat to feed from the slender, 80–90 mm long corolla of the flowers of *Centropogon nigricans*. No other animal has been recorded visiting the plant, suggesting that it is probably the only pollinator.

Interactions between predator and prey have led to a continual 'arms race', with the prey evolving better means of escape, and the predator, of necessity, overcoming them in the fight for survival. This
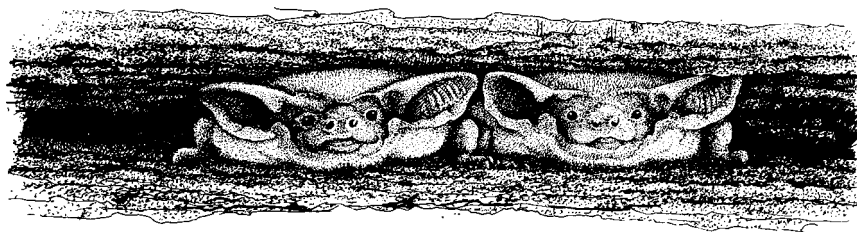
The flat headed bat, *Sauromys petrophilus*

arms race is nowhere better illustrated than in the relationship between bats and their insect prey. Noctuid moths, for example, have evolved 'ears' to detect approaching bats and have stereotyped avoidance mechanisms hardwired into their nervous system. Some bats have evolved echolocation calls that are less audible to moths, or catch them without using echolocation. New and increasingly subtle adaptations are uncovered almost every year. There is also evidence for arms races between bats and *their* predators.

Few cited examples of reciprocal altruism are clear cut and beyond explanation in terms of kin selection. One exception appears to be blood sharing in the common vampire bat (*Desmodus rotundus*). Vampires must have their 25 ml blood meals on a regular basis to survive, and in close-knit groups within a colony bats will regurgitate some of their last meal to a 'buddy' who has been unable to feed. From studies of the behaviour of wild bats in the roost, and of captive bats whose degree of relatedness was known, it appears that this behaviour of vampire bats is truly altruistic and cannot always be explained on the basis of kin selection. The system works because the donor will only give if the benefit to the recipient is far greater than its own loss, and because the favour is returned at a later date.

The Phyllostomidae (New World leaf- or spearnosed bats) are the family to go to for a lesson in adaptive radiation. The family contains about 160 species in 55 genera. They are fewer and far less widespread than the Vespertilionidae or evening bats, but are unmatched in the range of food they eat. Many species are insectivorous, like all in the ancestral family, but there are now large numbers of fruit, flower, nectar and pollen-eaters, carnivores,

and three species of vampire bat. This diversity of feeding habits is paralleled by a fine display of variations in form, physiology, and ecology—the long and bristly tongues of nectar feeders, the white tentmakers, the record-breaking kidneys of vampires, and the chin-flap-cum-night-cap of the wrinkle-faced bat.

Over the last 20 years several areas of research have exploded into activity with the rapid development of molecular genetics and easy access to user-friendly and powerful computing. They have given us powerful tools to investigate, among other things, the evolutionary origins of bats and their ability to fly and echolocate, historical distribution patterns, and the complex social lives of bats. For example, the consequences of the most recent glaciations and the role of mountains as barriers to post-glacial recolonization are being revealed by an analysis of current population genetic structure. The subtle adaptive value of the complex social life of the greater horseshoe bat is being unravelled by genetic analysis over many generations.

The abundance and diversity of bats makes them good models in the fields of biogeography and macroecology and this is another area that has seen a rapid expansion in recent years. Studies of bats are helping us understand the rules that govern the distribution of life on the Earth, such as species–area relationships and the ways in which latitude and elevation determine the richness and abundance of life.

Sadly, much of this fascinating diversity is under threat. Bats are subject to the same pressures as the rest of life on the planet—relentless human pressure leading to habitat degradation, fragmentation, and loss. They are also subject to some more or less unique problems because of

their life history strategies. Their tendency to form large aggregations for breeding and hibernating, often in close proximity to humans, make them particularly vulnerable. Their low reproductive rates make them slow to recover from population decline. The driving force behind much current research is conservation: a desire to understand bats so that we are better able to protect them. We are learning more and more about their fascinating biology and their ecological roles as pollinators, seed dispersers, and pest controllers—and we are taking the messages learned to a wider audience; the public image of bats is also improving. This is an important part of the conservation effort. A growing understanding and appreciation of the ecological role of bats, and a fascination for their unique biology, must make conservation easier.

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CHAPTER 1

Evolution and diversity

Fossils and what they tell us about the origin of bats. Molecular genetics tells us more about the evolutionary history of bats. Why did bats evolve? The origins of flight and echolocation. Past controversies, the current concensus and the implications to bat evolution. A brief classification of modern bats. Brief descriptions at family level. The Phyllostomidae—an example of adaptive radiation.

Evolution

Fossils and the origins of bats

Bats are the second largest mammalian order. There are an estimated 1,116 species and the number grows annually as new species are named, primarily through the splitting of existing species based on genetic evidence. They have long been divided into two sub-orders, the Mega- and Microchiroptera, commonly referred to as the megabats and microbats. The justification for these two sub-orders, as we will see, has recently been undermined, and the terms now have to be interpreted differently. I will define them and continue to use them where appropriate in this chapter, since they have historical and biological significance and you will find them widely used in the literature. However, as these two terms are now obsolete I will endeavour not to use them after this chapter! The megabats are the Old World fruit bats: often large (for bats that is, at 20–1,500 g), exclusively plant-eating (they eat mainly fruit, flowers, nectar, and pollen), and confined to Africa, tropical Asia, and Indo-Australasia. As I write there are 186 known, living species, all belonging to one family, the Pteropodidae. Microbats on the other hand are found on every continent except Antarctica, and, like the megabats, on many isolated islands. They are generally smaller than megabats (1.5–150 g), and they eat all sorts of things, although the ancestral microbat almost certainly ate insects and other arthropods. The 930-plus species are distributed among 17 or 18 families. Until quite recently this division into sub-orders was largely

unquestioned and, controversially, it had even been suggested that they might have different ancestors. The resolution of this controversy has led to some surprising results, which will be discussed in detail later in the chapter. For the moment you will have to take the phylogenetic tree in Fig. 1.1 on trust. It shows the known fossil bats in relation to extant bats, and a number of other mammalian orders: note that the traditional sub-orders have disappeared.

It is generally said that bats are not well represented in the fossil record. There is no shortage of species, just a shortage of anything more than jaws for most of them, and the ratio of known extinct to living species is low in relation to other mammals. Nevertheless, fossils of almost 200 species have been found. There are fossil representatives of all modern families except Rhinopomatidae and Craseonycteridae, in addition to fossils of species from a number of long lost families. Most fossils are too recent to shed much light on the origins of bats, but several do date back to the Eocene.

What do the earliest fossils tell us about bat evolution? The answer is surprisingly little. The oldest fossil bat, *Icaronycteris index*, was found in the Green River, Polecat Bench formation of Wyoming, not far from Yellowstone Park in the United States, and has been dated to the early Eocene, 50 million years ago (Jepson 1966, 1970). *Icaronycteris* looks remarkably like a modern insectivorous bat. The best European specimens were found in the famous oil-shale pits at Messel, near Darmstadt in Germany: *Archaeonycteris*, *Palaeochiropteryx* (Fig. 1.2), and *Hassianycteris* (Smith and Storch 1981). Preservation is
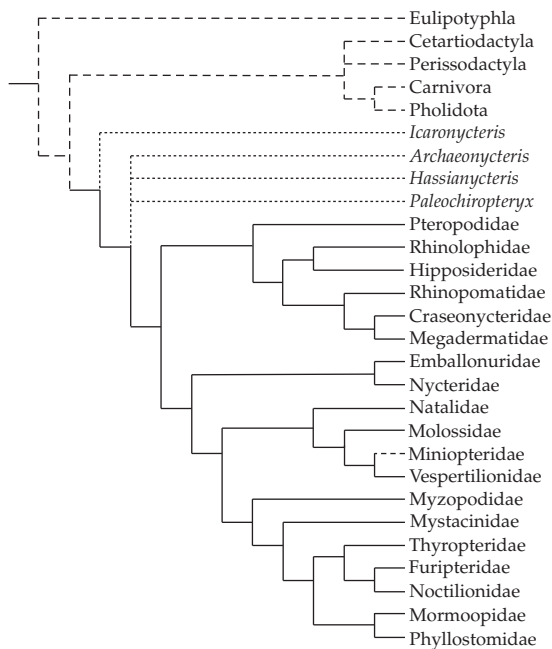
Figure 1.1 An evolutionary tree of modern and fossil bats. Adapted from Teeling *et al*. (2005), with permission from AAAS. At the top (dashed lines) are the relationships to a number of other mammalian orders, the Eulipotyphla (insectivores), Cetartiodactyla (whales and relatives), Perissodactyla (odd-toed ungulates—horses, etc.), Carnivora (carnivores), and Pholidota (pangolins). The dotted lines denote extinct bats. The Miniopteridae have until recently been included in the Vespertilionidae. Fossils are lacking only from the Craseonycteridae and Rhinopomatidae.

Figure 1.2 *Palaeochiropteryx tupaiodon*, an Eocene fossil bat from Messel in Germany.

so good that recognizable insect remains can be seen in the gut of some specimens. On the fossilized wingscales of moths eaten by the bats, identifiable pollen grains can be seen—evidence of where the moth took its last meal—ecology captured in stone! All of these bats date back about 45 million years, and all resemble modern bats. A lavishly illustrated book has been published on the Messel beds, with superb photographs of these bats (Schaal and Zeigler 1992). It is now sadly out of print, but well worth finding in a library. No fossil bats were known that were in any way intermediate in form between a modern bat and some early, tree-living ancestor which might have got around by jumping or gliding. However, if we allow time for the evolution of these sophisticated aerial insectivores, with an apparently advanced echolocating capability, then bats probably made their appearance over 65

million years ago. If so, they shared the world with the dinosaurs, and watched their extinction at the end of the Cretaceous.

What evidence can we cite in support of this time scale? Until recently there was little evidence of real substance, but some of a persuasive, if circumstantial, nature. As we'll see a little later, bats show no close affinities to any other mammalian order: according to the latest analyses (Murphy *et al*. 2001 and Fig. 1.1), their nearest, but still distant, relatives include the pangolin and the horse! These are unlikely ancestors for the bats, and they probably evolved from something resembling modern tree shrews. This early inability to link bats to any known mammalian group in itself suggested a very early origin and prompted a more oblique search for clues. Some moths, mantids, lacewings, and other insects have 'ears' whose main function appears to be to detect the echolocation calls of bats and trigger escape responses (Fullard 1987, Bailey 1991). Gall and Tiffney (1983) discovered the fossilized egg of a noctuid moth in deposits at Martha's Vineyard in Massachusetts which date back to about 75 million years ago. All known living and extinct

noctuids are tympanate, and their ears are tuned to the ultrasonic frequency range used by many echolocating bats. If the moth that laid this eggs was tympanate, then echolocating bats may already have been around 75 million years ago. Finally, there are a number of cases where closely related bat species live on now distant fragments of Gondwana. Before the break up of this southern supercontinent these bats presumably shared the same landmass. The break up started with the separation of Antarctica/Australasia from South America, and ended with the separation of Australia from Antarctica about 50 million years ago (Fig. 1.3).

New Zealand has just two endemic mammalian species, both bats. The closest living relatives of the short-tailed bat (*Mystacina tuberculata*) appear to be the fisherman bats (*Noctilio*) of South America (Pierson *et al.* 1986, Teeling *et al.* 2003). The more recent

100 Ma Reconstruction

75 Ma Reconstruction

65.0 Ma Reconstruction

47 Ma Reconstruction

Figure 1.3 The break-up of Gondwana. Plate fragments 100, 75, 65, and 47 million years ago are shown as solid blocks outlined in black. Current day shorelines are shown largely within the outlines of the old land masses. Small islands between Antarctica and New Zealand may have aided the movement of the ancestors of *Mystacina*. Adapted from maps available at www.odsn.de.

work of Teeling and colleagues is based on an extensive genetic comparison of *Mystacina*, *Noctilio*, representatives of twelve other bat families, and six mammalian outgroups. The ancestors of these two bats appeared to separate from other bats about 67 million years ago, probably in South America. *Mystacina* separated from *Noctilio* about 47 million years ago and probably dispersed to what was to be Antarctica and Australia. New Zealand had already started to drift away from the Antarctic–Australian Plate about 75 million years ago (Griffiths and Varne 1972), but had perhaps not travelled too far by 47 million years ago to prevent this migration, perhaps by island-hopping.

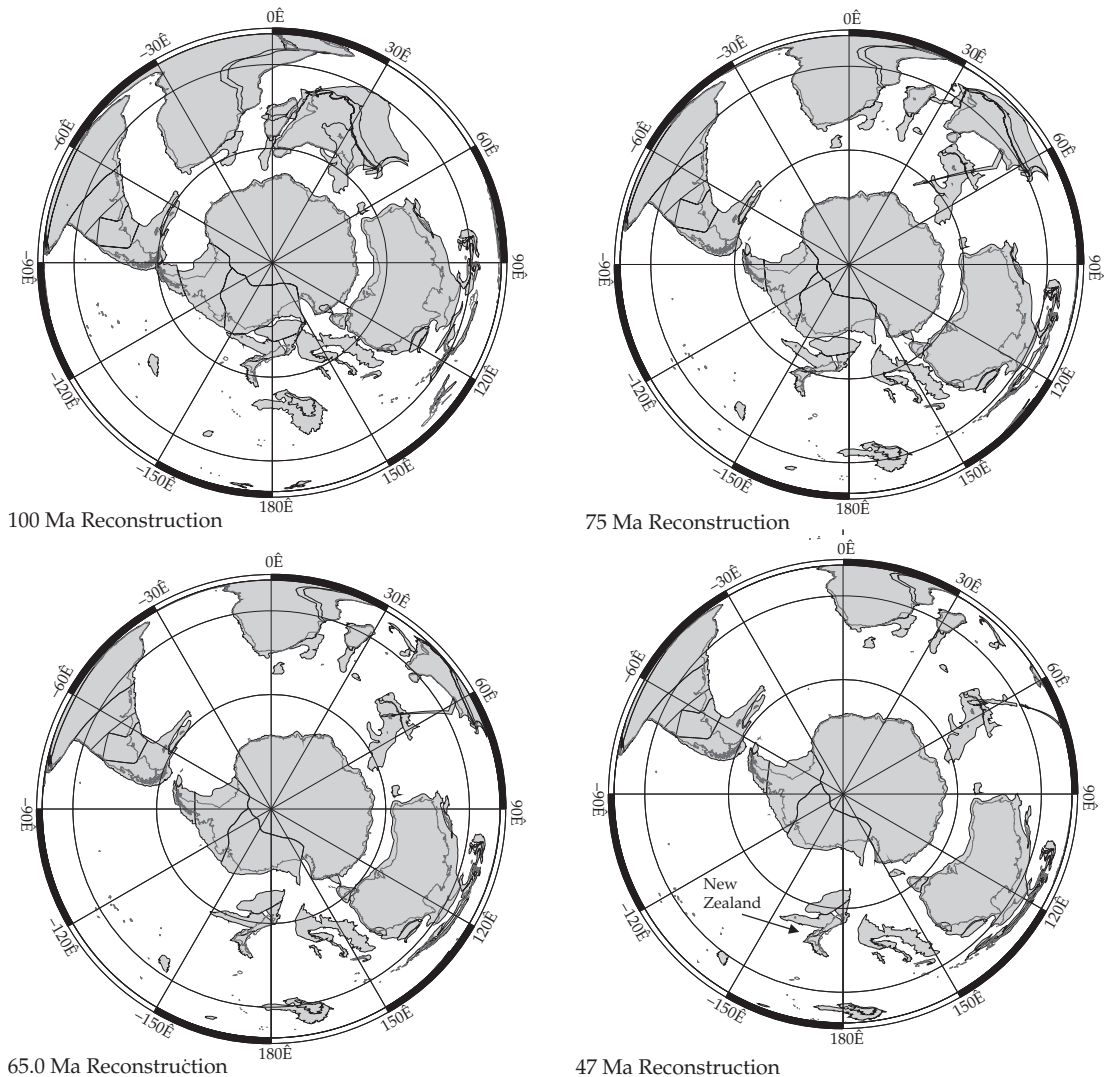That was the story when I thought I had finished writing this chapter and moved on to the next. But, not for the first time in the writing of this book, I was forced to go back and describe new developments. Simmons *et al*. (2008) have recently described a new and important fossil species, again from the Green River Formation in Wyoming. *Onychonycteris finneyi* is similar in age to *Icaronycteris*, but appears more primitive in several ways. The cochlea is proportionally smaller than in other Eocene bats, suggesting that echolocation was either poor or absent. The fingers in its short, broad wings are unique amongst bats in that all have retained their claws, and although it has an anatomy consistent with powered flight, it does appear to be primitive. Its limb proportions are intermediate between those of non-volant mammals and all known bats, including other Eocene species. This does not necessitate bringing the evolution of bats forward, but it does shed light on a number of questions. It shows, for example, that the claws on the third to fifth fingers were lost after the evolution of flight and that both the arm and hand bones continued to elongate, leading to more aerodynamically efficient wings. *Onychonycteris* may also shed light on one of the more debated questions about bat evolution: which evolved first, echolocation or flight, or did they evolve together? I'll leave that question until later.

The current picture–molecular genetics meets morphology

The appearance of sophisticated molecular techniques, and advanced methods for interpreting the complex data they produce, have led to a revolution in our understanding of how and when bats evolved. Figure 1.4 shows a basic molecular phylogeny of the bats (from Teeling *et al*. 2005) and where in the world the major groups are thought to have evolved. Figure 1.5 shows the estimated dates of the major radiations (Teeling *et al*. 2005). These results are based on over 13 kb of sequence data (13,000 base pairs of DNA sequence) from 18 nuclear genes and species from all known bat families were included in the study. Recently it has been suggested that all 19 species in the genus *Miniopterus* should be elevated to family status, the Miniopteridae (for example Hoofer and van den Bussche 2004), rather than be included within the Vespertilionidae. A re-analysis of the morphological data of Simmons and Geisler (1998) by Teeling *et al*. (2005) suggested that the four extinct Eocene families were closely related and sister taxa to all living bats. This tree is supported by that shown in Fig. 1.6 constructed by Eick *et al*. (2005) and based on a 4 kb sequence from four intron markers. Introns are non-coding sections of DNA situated between those coding for proteins. The analysis by Eick and colleagues included 58 species from all families except the Craseonycteridae. Eick *et al*. (2005) also attempted to look at the geographical origins of bats and, in contrast to Teeling *et al*. (2005), concluded that modern families had a southern hemisphere origin, probably in Africa. The molecular trees confirm an early origin for bats, with the last common ancestor about 64 million years ago and possibly earlier. The bats underwent a major diversification about 50 to 52 million years ago when all four major microbat lineages appeared. According to Teeling *et al*. (2005) they appear to have evolved in the ancient northern landmass of Laurasia, in what is now North America, before migrating and evolving across Laurasia and Gondwana to the south (but see Eick *et al*. (2005) for an alternative view). Their radiation arose from two newly identified suborders, the Yinpterochiroptera and the Yangochiroptera. The Yinpterochiroptera evolved in Asia and have an exclusively Old World distribution. The origins of the Yangochiroptera are less clear, but they too probably arose in Laurasia, in either Asia or Europe, but now have a global distribution which raises some interesting questions about dispersal.
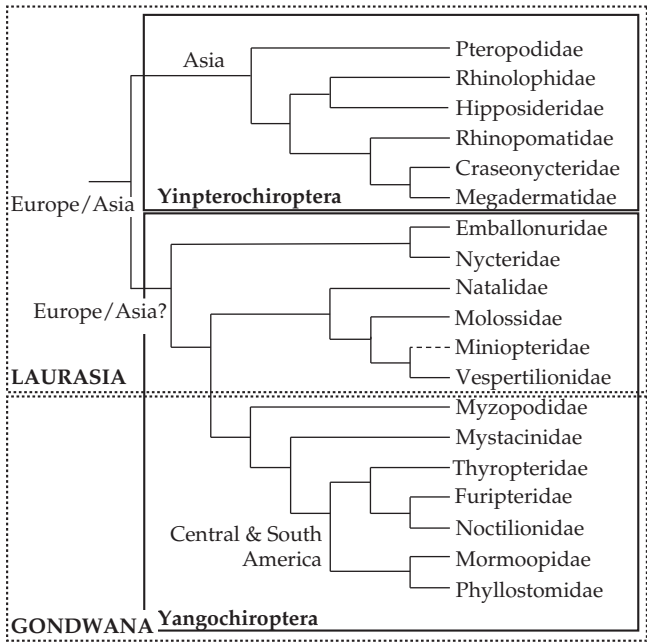
Figure 1.4 A molecular phylogeny of the bats showing where in the world the major groups were thought to have evolved. (Adapted from Teeling *et al*. (2005) with permission from AAAS.)
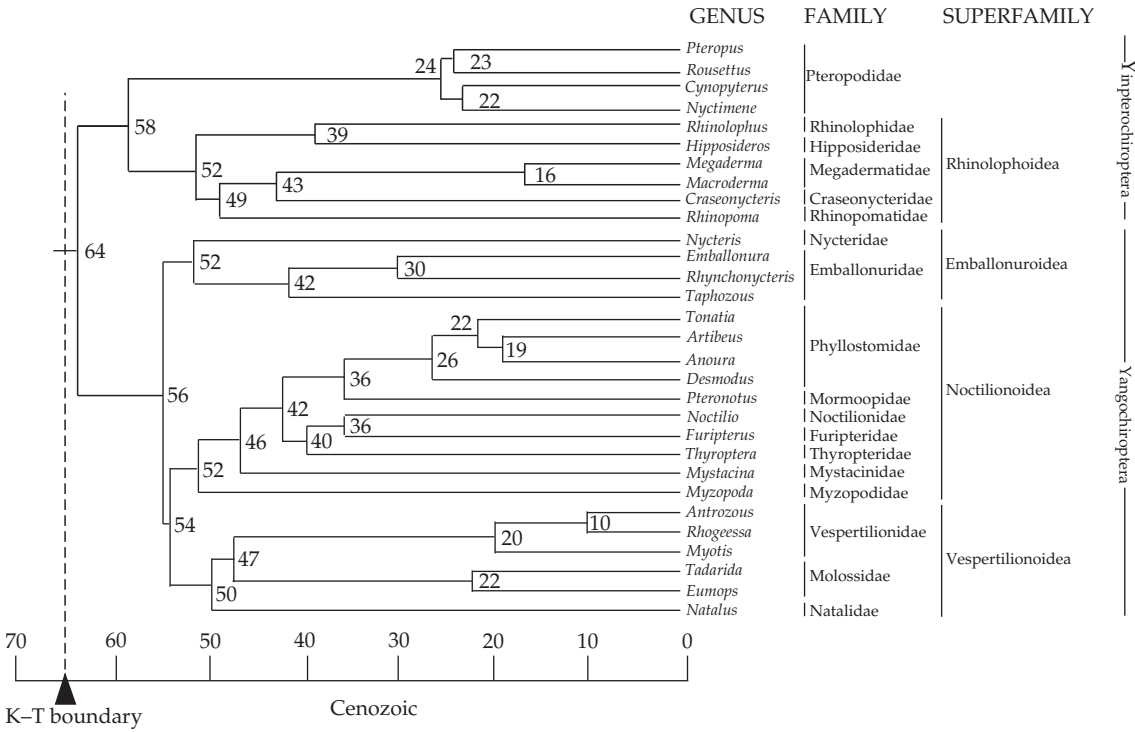
Figure 1.5 A proposed time scale for the evolution of the representatives of all but one (Miniopteridae) of the bat families. (Adapted from Teeling *et al*. (2005) with permission from AAAS.) All numbers refer to millions of years before the present. K–T boundary = Cretaceous–Tertiary boundary.
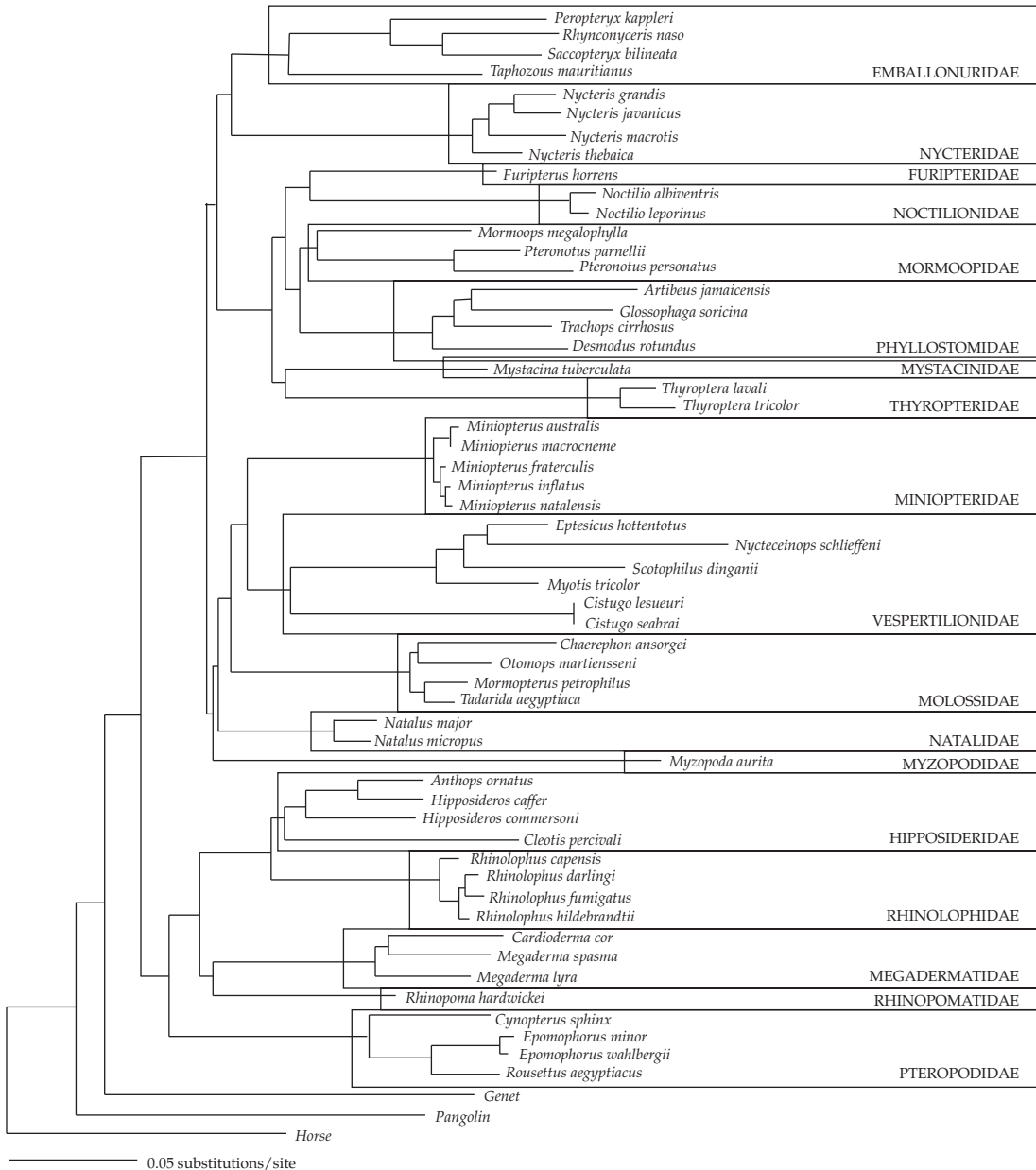
Figure 1.6 A phylogenetic tree derived from sequences of four intron markers by Eick *et al*. (2005). Note that the Craseonycteridae were not included in this study.

For example, did the New World emballonurids, which separated from their African cousins about 30 million years ago, cross the Atlantic from Africa on stepping stones or vegetation rafts as has been suggested for new world monkeys (Flynn and Wyss 1998)? Teeling *et al*. (2005) suggest that the noctilionoids arose in Gondwana, perhaps South America. Among them, the phyllostomids, mormoopids, noctilionids, furipterids, and thyropterids are largely confined to the neotropics, but the

two mystacinid species (one of them now extinct) are found only in New Zealand and the one myzopodid is an endemic of Madagascar! The two speciose families that make up most of the vespertilionoids, the Vespertilionidae and the Molossidae, both have global distributions and their place of origin is uncertain.

Why did bats evolve?

The evolution of new species is the product of the spontaneous generation of random genetic mutations and the forces of natural selection—often a response to a changing environment. Change means a new physical environment, new sources of food, new habitats, new competitors, and new predators. At the time bats are thought to have been evolving, the flowering plants were in the first stages of their massive diversification. Müller (1981) conducted a review of the pollen record and demonstrated a proliferation of angiosperms at all taxonomic levels. They became dominant over more primitive plants in the Cenomanian period (100–95 million years ago), and modern families appeared in great numbers from the beginning of the Maastrichtian (69 million years ago). By the end of the Cretaceous the insects supported by these plants were abundant and insectivorous and frugivorous mammals were becoming well established (Lillegraven 1974). Teeling *et al.* (2005) cite evidence for a 7 °C rise in mean temperature, a significant increase in plant diversity and a peak in Tertiary insect diversity that coincided with the appearance of the four major microbat groups. This progressive increase in insect diversity provided an abundant food source for bats and other mammals, but they didn't have them all to themselves. During the day, they would have had to compete with birds and other insect eaters. *Archaeopteryx*, the first bird, dates back to the early Cretaceous (135 million years ago), and birds were abundant by the time bats appeared on the scene. Birds were likely to be significant competitors and predators of small mammals by the late Cretaceous (65 million years ago). For these reasons many early mammals (like their modern counterparts) were nocturnal, and it is presumed that bats evolved from one of these small, nocturnal, and arboreal (tree-dwelling) mammals.

Gliding and flying

What follows is largely informed speculation, but I think few biologists would question it. Over thousands of years of jumping around after insects, from branch to branch, and tree to tree, the ancestors of microbats probably evolved gliding membranes similar to those of modern mammals like flying squirrels and sugar gliders (Fig. 1.7). We should not be surprised that this may have happened— gliding has evolved independently many times in the vertebrates, with living examples among the fish, amphibia, reptiles, marsupials, and eutherian mammals (see for example Rayner 1981).

Before going any further, we ought to ask the question: why did flight evolve? Two very powerful reasons come quickly to mind. Less energy is expended gliding from tree to tree than running down the trunk, running across the ground, and running up the trunk of the next tree. Furthermore, if the animal doesn't come down to the ground, it doesn't have to face terrestrial predators either. Controlled, flapping flight brings other advantages, discussed in Chapter 2.

Let's go back to the evolution of gliding. A narrow extension of the skin between front and hind legs probably became more extensive, and extended to the spaces between hind legs and tail. With the appearance of webbing between the fingers and toes, the fingers could elongate, carrying the webbing with them, dramatically increasing the wing area. A study by Sears *et al.* (2006) suggests that increased local expression of a single protein, Bmp2, which causes proliferation of bone forming chondrocytes, may have been a critical step in the evolution of the bat wing. It appears to have been a rapid evolutionary step, since the lengths of the third to fifth fingers have remained very similar in length (relative to body size) over the last 50 million years (with the notable exception of *Onychonycteris*, Simmons *et al.* 2008). By having its fingers within its wings the ancestral bat gained greater control over wing shape, giving it more aerial control. Ultimately wings used for gliding must eventually have begun to be used for active flapping flight, as the necessary neuromuscular, circulatory, and respiratory adaptations evolved (see Chapter 2).
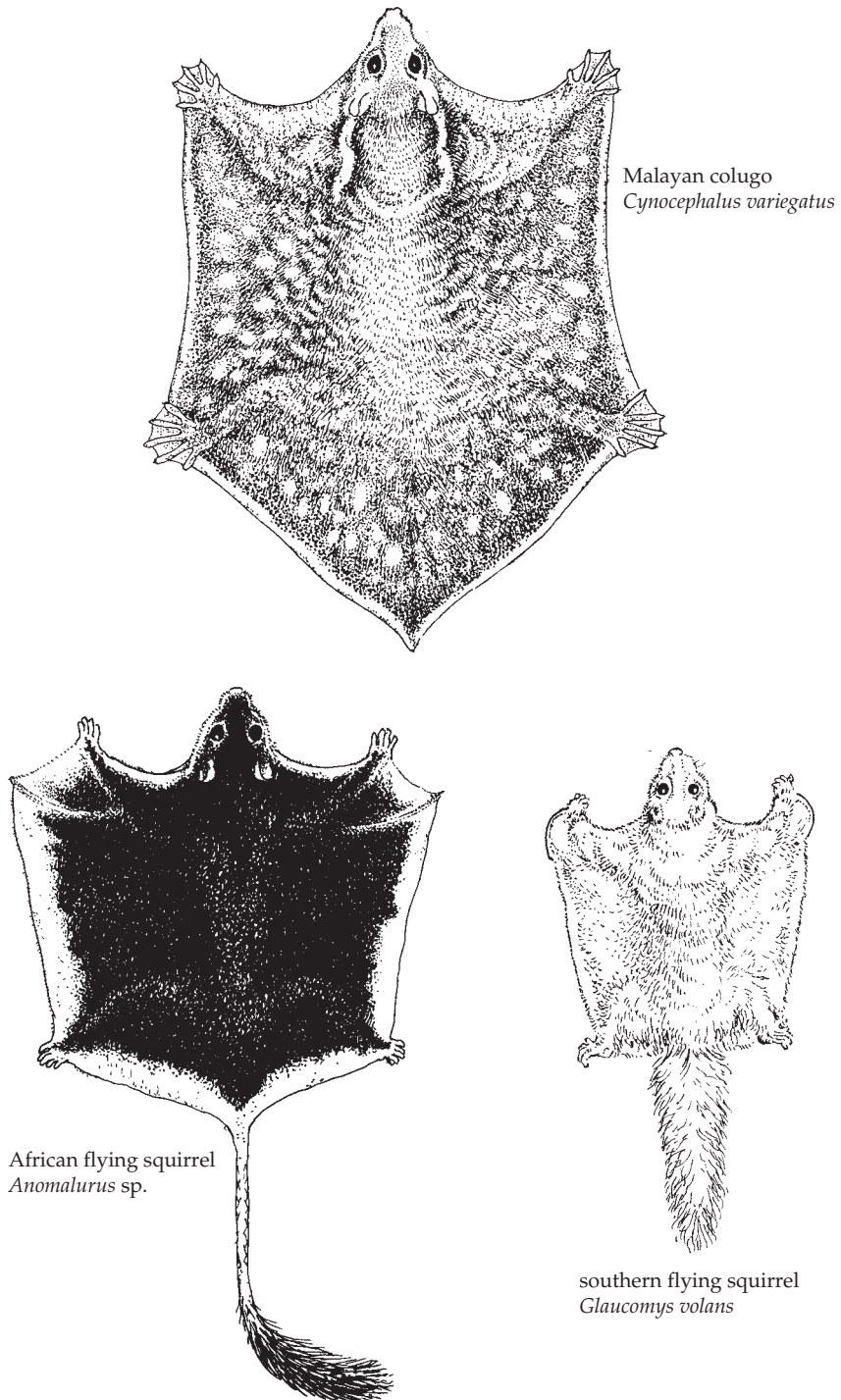
Malayan colugo
Cynocephalus variegatus

African flying squirrel
Anomalurus sp.

southern flying squirrel
Glaucomys volans

Figure 1.7   Modern gliding mammals.

Echolocation

As early bats became more agile, perhaps even before they became bats, they would have had to improve their orientation skills to be successful night flyers. Echolocation, orientation by analysis of the echoes from emitted sound pulses, probably increased in sophistication alongside flight. It is difficult to imagine how the two could have reached their present level of sophistication unless they coevolved, at least in the absence of good night vision. It is likely that the ancestors of bats, like some modern insectivores, emitted ultrasonic sounds and perhaps had a simple form of echolocation, which became increasingly sophisticated as bats became more agile flyers. Novacek (1985) produced evidence to suggest that the very early fossil bats, *Icaronycteris index* and *Palaeochiropteryx tupaidon*, had a well developed echolocation system—perhaps better developed than that of some modern bats. This evidence came from a study of the internal structure of the fossil skulls. The single most important feature is the large size of the basal turn of the cochlea—the structure in the inner ear which sorts and processes sounds by frequency. The basal turn is receptive to the echoes of very high frequency echolocation calls.

The size of this basal turn will obviously depend upon the size of the bat, but when these two parameters were plotted against each other, so that the size of the basal turn was shown relative to the size of the bat, *Icaronycteris index* and *Palaeochiropteryx*

tupaidon both fell in the middle of a cluster of data points for modern echolocating bats. For their size, their basal turns appeared to be as well developed as those of most modern bats. However, a later analysis of a more extensive data set tells a different story (Habersetzer and Storch 1992). Figure 1.8 shows basicranial (skull) width (skull length, as used by Novacek (1985), may depend on feeding strategy) plotted against cochlea diameter for the Eocene Messel bats. They have cochleas similar to, or smaller than, the smallest of the Vespertilionidae, bridging the gap between echolocating insectivorous bats and the non-echolocating Old World fruit bats. A number of the extant echolocating bats studied fall in the same area: all of them have foraging strategies which make use of vision, olfaction, or prey-generated sound, in addition to echolocation. In other words, they do not depend entirely on echolocation. This suggests that the cochlear system of the Eocene bats was not as advanced as that of modern insectivorous bats, and that they too did not rely exclusively on echolocation. The recently discovered Eocene bat *Onychonycteris* (Simmons *et al.* 2008) not only has a small cochlea, but lacks other features, present in *Icaronycteris* and *Palaeochiropteryx*, that suggested to the authors that it may not even have been able to echolocate. More recent work by Veselka *et al.* (2010) on the structure of the larynx suggests otherwise—this is an area of intense research that I will return to in Chapter 3.
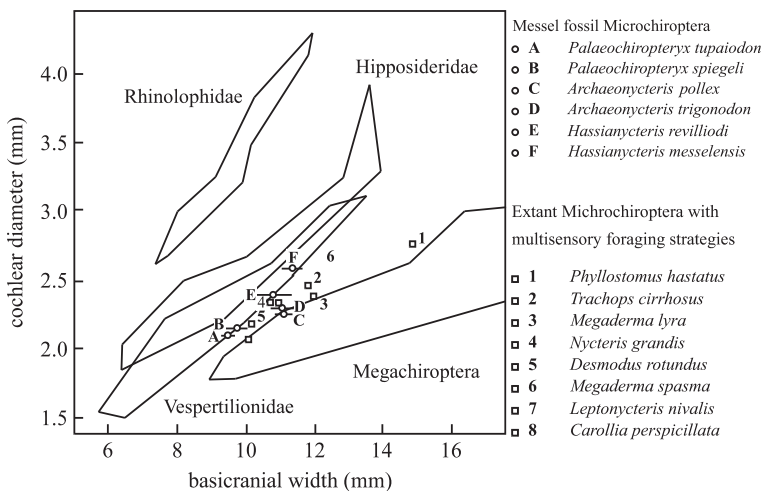

Figure 1.8 Cochlear size and echolocation. The relationship between the width of the cochlea and skull width for a sample of 6 Eocene and 286 extant species. (Based on Habersetzer and Storch 1992.)

Note in Fig. 1.8 that there is little overlap between the megabats and microbats. All microbats use echolocation at least some of the time, even those that feed on fruit and nectar. Amongst megabats, only a few species from the genus *Rousettus* echolocate, using a very different and probably less capable method. Most bats generate their echolocation calls in the larynx, but *Rousettus* do it by clicking their tongues. Why the difference? If the oldest fossil bats are echolocators, why don't the megabats use echolocation? It seems remarkable that not only may they have lost the ability to echolocate, but that they also appear to have lost the anatomical and physiological adaptations which made it possible. In the 1980s this observation led scientists to ask the question: did all bats really have a common ancestor? The question had been asked before, but only at this point did the tools exist to address it in depth.

The evolution of bats: a recent debate and a new consensus

The last 20 years have seen the birth and death of a major controversy in bat evolution and phylogeny. It would be simpler and easier to pass over this and describe the current state of affairs, but we would miss out on an interesting and informative debate, so we'll start at the beginning and see how the investigations unfolded. The modern colugos, or flying lemurs (Fig. 1.9), resemble in some respects

our hypothesized ancestral bat, since they have an extensive gliding membrane and webbed fingers.

They are not lemurs, but dermopterans, and they do not fly, but glide. The two living species are the only dermopterans. Colugos can glide well in excess of a 100 m, and move their limbs around to turn and change altitude. In one recorded glide of 136 m, an individual lost only 11 m in altitude. They are herbivores the size of a small cat and their adaptations to gliding have left them clumsy on the ground. For a long time they were assumed to provide a useful illustration of how bats might have evolved. Someone then suggested that they were not just a useful illustration, but perhaps real ancestors to the megabats.

The earliest megabat is *Archaeopteropus transiens*, which dates back 35 million years to the Oligocene (36–25 million years ago) and was found in Venetia, Italy (Dal Piaz 1937). Until the 1980s it was widely accepted that all bats had a common ancestor. However, it was then suggested that the megabats evolved independently, following a quite different evolutionary line to that of the insectivorous microbats. A strong body of evidence in support of this idea was put forward, triggering a very vigorous controversy and new research. It is worth discussing in some depth for several reasons. First, to dispel the common idea that taxonomy plays little part in modern biology. Second, to show that answers to many important biological questions only come with input from a wide variety of fields–biology is
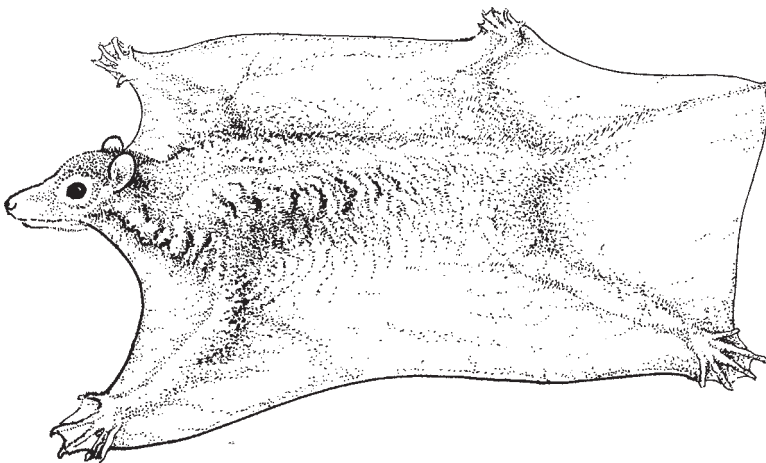

Figure 1.9 A gliding dermopteran (flying lemur).

a truly multidisciplinary subject. Finally, because of the implications of independent origins for microbats and megabats—principally that flight, the most anatomically and physiologically specialized and demanding mode of locomotion, evolved twice in the mammals, and that the striking similarities between microbats and megabats are the result of convergent evolution. We have already noted the absence of echolocation and the small cochlea in megabats. What other evidence was put forward in support of diphyly (independent origins) in bats, and what evidence is there for monophyly (common origins)?

This debate had in fact been around for some time (see for example Jones and Genoways 1970, Smith and Madkour 1980) but it gained momentum with the publication of a paper (Pettigrew 1986) which suggested that the pattern of neural connections between the mid-brain and the retinal cells of the eyes were very different in microbats and megabats.

All neurones in the right superior colliculus (s.c.) of the mid-brain appeared to project to the retinal cells of the left eye of a microbat and those of the left s.c. to the right eye (Fig. 1.10). This pattern has been found in all mammals except primates, and is believed to be the ancestral mammalian pattern. In contrast, neurones from the right s.c. of a megabat project to both eyes, but only to the left half of the visual field. Neurones from the left s.c. projected to the right half of the visual field of both eyes. This pattern was thought to be unique to primates, but

Pettigrew (1986) found it in megabats and Dermoptera. He argued that it was highly unlikely that either of these two patterns could have evolved from the other, suggesting that microbats and megabats are not at all closely related, but that megabats were in fact 'flying primates'. It is interesting to note at this point that in 1758, after studying megabats, Linnaeus originally classified bats as primates. Subsequent evidence which showed that microbats were not related to primates resulted in all bats being reclassified.

Pettigrew *et al*. (1989) went on to show, through a cladistic analysis of some 24 different characteristics of the nervous systems of 14 mammalian species, that microbats appeared very early in mammalian evolution, and that their nearest relative *among the mammals studied* was the tree-sloth *Bradypus*! Megabats appeared to have evolved much later, from an early primate branch, around the same time as the Dermoptera. The cladogram is shown in Fig. 1.11. A cladogram is a form of evolutionary tree which links species according to shared, **derived** characteristics. That is, those characteristics that are not ancestral to all of the species in the group being studied, but evolved after their divergence from a common ancestor. The more characteristics shared between two species, the more closely related they

Figure 1.10 Simplified diagram of the primitive/microbat (left) and primate-like/megabat (right) connections between the mid-brain (superior colliculi) and the eyes (Based on Pettigrew *et al*. 1989.)

Figure 1.11 Cladogram based on the analysis of 24 neural characters. The megabats *Pteropus* and *Rousettus* appear to be closely related to the primates and dermopterans and are separated from the microbats, *Macroderma* and *Mormopterus*, by several other taxa. (Based on Pettigrew *et al*. 1989.)

Box 1.1 Cladistics

The philosophical framework of modern taxonomy is based on the concepts of evolutionary theory. Cladistics was developed in an attempt to introduce a set of more objective and rigidly applied rules than those used in traditional evolutionary taxonomy (Hennig 1966). In cladistic analysis, given a group of animals to classify, the first and most crucial task is to sort out which forms of a particular character are ancestral and which are derived. There are three lines of evidence, but it is rare to be able to use all three in any particular case.
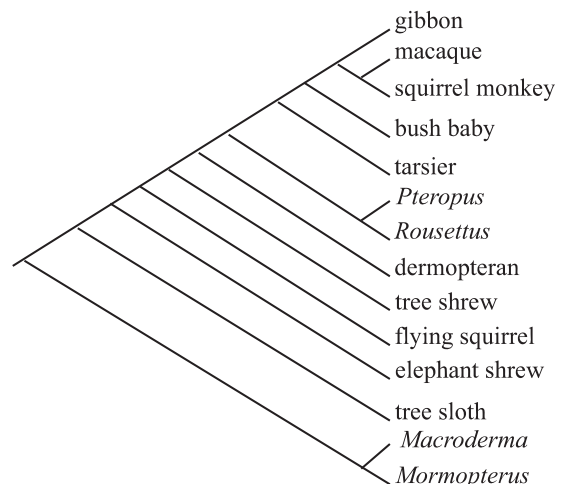
1. *Outgroup analysis*. A comparison of characters with those of another species, or group of species, which is known not to belong to those under study, but which is relatively closely related. Any shared characteristics are by definition ancestral. It sounds fine in principal, but it requires prior knowledge of the relations between groups. This has led some people to criticize the technique as circular. This is an unfair simplification, and it would be more realistic to view it as part of an iterative process—constant refinement of the model to arrive at an answer that best fits the known facts—a perfectly valid scientific technique. Another criticism is that the method assumes that there is no evolutionary convergence, or at least that it is rare. The problem is one of separating homologous structures, that is those with a common origin, from analogous structures, which are derived from different parts of the body but serve a similar function. Good examples of convergent evolution, and analogous structures, are the wings of birds and insects and the eyes of vertebrates and cephalopods. Convergence probably is rare, but when it does occur it will lead to errors in cladistic analyses: but then it can upset traditional methods too.
2. *Palaeontological evidence*. A good fossil record will provide good evidence of which characters are ancestral and which are derived. However, fossil records are usually full of gaps, and many characters are simply not preserved in fossils. The technique therefore has limited practical value in many cases.
3. *Embryological evidence*. It is assumed that in the embryological development of a group of species, the general, ancestral characters appear before the more specialized, derived characters. This assumption is certainly not valid all of the time. The big debate concerns the frequency with which it is valid. It is perhaps safest to say that any evidence drawn from embryology should be used with some caution.

Given the difficulties, it is clear that cladistics must use all of the techniques at its disposal and cross-reference wherever possible. The use of **unrooted** trees can help greatly. An unrooted evolutionary tree indicates the relationships within a group of animals, but does not indicate the order of their evolution. Unrooted trees can be constructed first on morphological or biochemical evidence, and **rooted** later, if key evidence can be found. Once a root has been found, the direction of the tree's 'growth' is known, and the evolutionary relationships between the species can be resolved.

Finally, in constructing cladograms, the various methods and computer programs used are generally based on the concept of parsimony. The tree that uses the least number of evolutionary steps and the smallest number of assumptions to explain the data is sought. This is not necessarily the way nature works, it is simply a practical scientific approach—that of Occam's razor. Other approaches are constantly being developed, such as maximum likelihood methods, and these may lead to different conclusions. Good basic accounts of cladistic theory and methods, and the debates surrounding them, can be found in Ridley (1986) and Patterson (1987) and for a more recent practical guide you might look at Forey *et al*. (1998). Whatever you read, it will be out of date unless you go to the primary literature, since this field changes constantly as new methods and programs are developed.

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are. A cladogram is constructed by computing the evolutionary tree which uses the least number of evolutionary steps to explain the different degrees of relatedness between the species. Cladograms can be very persuasive, but have their problems. For those interested, Box 1.1 takes a closer look at cladistic techniques, since they are now widely used in evolutionary biology by the traditional morphologist and, as we will see below, the molecular taxonomist.

The argument that primates, dermopterans, and megabats are closely related, and that microbats are unrelated to megabats, was strengthened by additional lines of evidence, from factors as simple

as a consideration of body size ranges, to the analysis of the amino-acid sequence of haemoglobin. Table 1.1 lists some of the differences between megabats and microbats not discussed in the text (Pettigrew *et al*. 1989). At the time this was countered by the evidence in Table 1.2, which lists features common to mega- and microbats, but not found in other mammals. It was these known differences that led to uncertainty, and started the controversy.

The research that was prompted by this work goes on still, but in the eyes of most scientists the debate is over. It is now widely accepted that bats are monophyletic and researchers are concerned with other evolutionary questions. The primary tool is molecular genetics, and one of its first uses was to drive the last nails into the coffin of the 'flying primate' hypothesis. I will come to that later, but I first want to show how we got to that point. In the early stages of the debate a wide range of approaches were used to provide evidence for both sides of the argument. Some of this is presented below, to show how the controversy progressed and how persuasive both sides could be. In the end, most of the evidence in favour of diphyly was undermined, but some of the issues raised are still debated.

One feature that was used persistently to argue for a close relationship between megabats and microbats was the similarity of their wings. The first part of Table 1.2 lists just a few of those cited by Baker *et al*. (1991): the wings of megabats and

Table 1.1. Some of the differences between megabats and microbats not covered in detail in the text. Discussed by Pettigrew *et al.* (1989).

	MICROBATS	MEGABATS
distribution	worldwide	palaeotropical (Old World tropics)
orientation	primarily by echolocation, all species generate sonar pulses in the larynx	primarily visual, tongue clicking orientation sounds produced by a few species only
diet	ancestral insectivores, a small minority have evolved to feed on fruit, nectar and pollen, vertebrates, and blood	fruit, nectar, and pollen
teeth	W-shaped cusps, or evidence for past possession of such teeth	simple, no evidence of W-shaped cusps (i.e. of insectivorous ancestry)
eyes	simple retinal blood circulation; tapetum lucidum (reflective layer behind receptor cells) rarely present; ganglion cell streak below optic disk; eyes open after birth	complex retinal blood circulation; tapetum lucidum often present; ganglion cell streak above optic disk; eyes open before birth
ears	pinna (external ear) often complex, margin incomplete; tragus (cartilaginous projection) often present inside pinna; Paaw's cartilage in middle ear cochlea (sound reception and processing apparatus in inner ear) variable in size and often large; cochlea has large, extra basal turn for high frequency sound reception; cochlea acoustically isolated from skull	pinna simple, margin complete to form a tube; tragus never present; Paaw's cartilage absent; size of cochlea closely related to size of bat; extra turn absent; cochlea in contact with skull
limbs	metacarpals (palm bones) long in relation to first phalanges (finger bones); thumb and forefinger have minimal independent mobility; limbs move independently, many species very agile on the ground	metacarpals and phalanges similar in length; opposable thumb and mobile forefinger; forelimbs move together, movement is slow and clumsy
skin	hair erector muscles are striated (like skeletal muscle)	hair erector muscles are smooth (like those of internal organs)
penis	corpus spongiosum not enlarged to form glans penis	corpus spongiosum enlarged to form glans penis
torpor	widespread in two families and highly developed	poorly developed, and only found in nectar feeders
roosting posture	neck extended (head bent towards back)—neck vertebrae specially adapted	neck flexed (bent towards chest)
threat behaviour	primarily acoustic, wing spreading not seen	often involves wing spreading and other visual threats
central nervous system	inferior colliculus (auditory centre) larger than superior colliculus (visual centre); primitive pathway between eye and brain; forebrain usually less well developed than hindbrain; low frequency sounds map at rear of auditory cortex; motor cortex shows primitive arrangement of cortico-spinal areas; hindlimb is represented by a small area of somatosensory cortex	superior colliculus larger than inferior colliculus; primate-like pathway between eye and brain; forebrain well developed as cerebral cortex; low frequencies map at front of auditory cortex; motor cortex shows primate-like arrangement of cortico-spinal areas; hindlimb is represented by a large area of somatosensory cortex

Table 1.2. Some of the characteristics shared by microbats and megabats. For detailed coverage, see Baker *et al*. (1991).

Anatomical features common to microbats and megabats

Occipito-pollicalis muscle along the leading edge of the wing
Fingers 2–5 of forelimb greatly enlarged
Claws restricted to digits 1 or 1 and 2
Hindlimbs rotated 90 ° outward, i.e. knee directed to the side
Calcar present on foot
Head of the femur aligned almost parallel to the shaft
Premaxilla greatly reduced
Jugal greatly reduced
Several anatomical features of the middle ear
Anatomy of preplacenta and placenta
Somatosensory map of forelimb reversed relative to other mammals

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microbats certainly do look very similar. However, this is to be expected since there is considerable similarity in mode of flight, and therefore in the evolutionary pressures moulding wing shape. Flying is not easy. There are few ways in which the vertebrate body plan can be adapted to meet the intolerant energetic, mechanical, and aerodynamic demands of flight. Pettigrew and his colleagues argued that wing morphology in fact yields evidence for the independent evolution of megabats and microbats, and for the close relationship between megabats, primates, and dermopterans. The hypothesis put forward was that the relative lengths of the bones of the third and fourth fingers are not going to be important in determining flight performance, and are therefore not subject to the evolutionary pressures of flight. (Finger 5 is known to play an important role in altering wing camber and was excluded from the analysis.) We might expect these fingers to be similar in all bats, or at least for no clear pattern to emerge between groups, if all bats are closely related.

This was not found to be the case. In Fig. 1.12 the ratios between the length of the metacarpals and the first phalanges of fingers 3 and 4 for a large number of megabats and microbats have been plotted against the forearm length of each species. There is no overlap between the data for microbats and megabats: the microbats have proportionally longer metacarpals. Can it be argued that the wings of megabats and microbats are so very similar? The relationship holds true for the hindlimb too, which

is under very different functional constraints. The dermopteran *Cynocephalus*, and the oldest megabat fossil, *Archaeopteropus*, fall among the megabats, as do primates. The ratio for the forelimb is very variable in microbats, but shows little variation in megabats: but then all of the latter belong to a single family.

By the same argument against functionally important morphological characters, the muscles of the wing should also be excluded from the list of supporting evidence for monophyly. The specialized occipito-pollicalis muscle complex (which controls the shape of the leading edge of the wing) was cited as evidence for monophyly (Wible and Novacek 1988), but it is present not only in microbats, megabats, and dermopterans, but also in the clearly unrelated flying squirrels (Johnson-Murray 1977) and birds (Raikow 1985). Thewisen and Babcock (1991) presented us with an interesting twist to this story. They looked not at the muscle complex, but at its pattern of innervation. If the occipito-pollicalis muscles are truly homologous rather than analogous they should have similar innervation patterns due to the close link between the development of a muscle and its nerve supply. (Homology: derived from the same ancestral muscles; analogy: convergent evolution leading to similar structures derived from unrelated muscles). Thewisen and Babcock found that features of the innervation pattern were quite unique among mammals, and common to microbats, megabats, and dermopterans: good news for the proponents of monophyly.

Molecular studies

Early molecular evidence in taxonomy came from immunological studies, to be followed by protein sequencing, and finally the sequencing of DNA itself. Like the morphological evidence, it has been controversial. Several early studies (for example Ammerman and Hillis 1992, Bailey *et al*. 1992) came down firmly on the side of monophyly, but Pettigrew (1994, 1995) questioned the validity of some of the base alignments which lead to this conclusion, and raised another complication. He argued that megabat DNA was rich in the nucleotide bases A-T at the expense of G-C. It was suggested that an
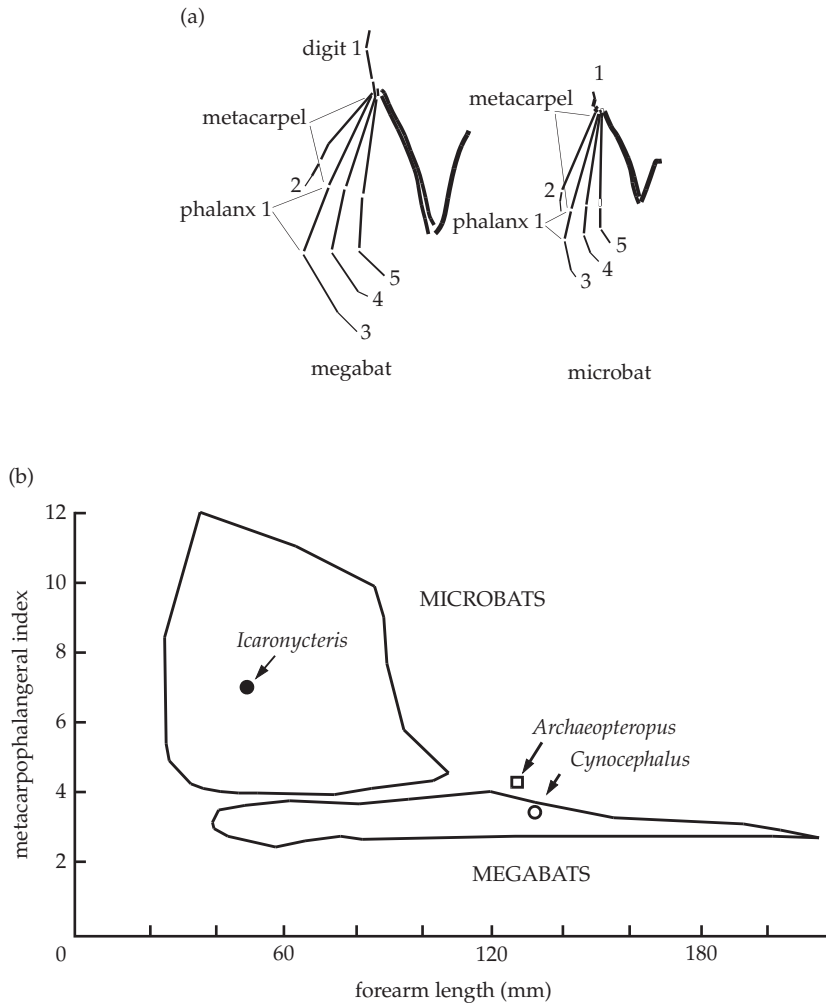
(a)

(b)

Figure 1.12 Forelimb morphology in bats. (A) The forelimb skeletons of megabats and microbats. (B) The ratio of metacarpal length/first phalanx length (for fingers 3 and 4), plotted against forearm length for a large sample of microbat and megabat species. A fossil microbat, *Icaronycteris*, and megabat, *Archaeopteropus*, and the dermopteran *Cynocephalus* are also included. (Based on Pettigrew *et al.* 1989.)

A-T content of more than 70 per cent, as was found in megabats, raised doubts about the validity of sequencing evidence, which assumes A-T and G-C are equally abundant. More recent studies did not find a high A-T bias in the genes sequenced and used methods that took into account the moderate heterogeneity in base composition that was observed. A major turning point came with the first of a series of papers by Teeling and colleagues (Teeling *et al.* 2001). They carried out a phylogenetic analysis based on four nuclear and three mitochondrial genes (a total of over 8,000 base pairs). Sixteen bat species were used, with representatives from all microbat superfamilies, megabats, and four outgroups (human, flying lemur, dog, and mouse). After rigorous analysis using the latest approaches and tools (see Box 1.2) they were able to reject the 'flying primate' hypothesis and found no evidence to suggest that the Dermoptera were a sister group to the bats. If this was not significant enough, they

came up with an even more startling result. The more observant reader will have spotted it already in earlier figures: the bats in the superfamily Rhinolophoidea are more closely related to the megabats than they are to other microbats. The implications of this are as profound as those of the 'flying primate' hypothesis. If true, then either the echolocation systems of the rhinolophoids evolved quite independently of those in other microbats, or they were lost in the evolution of the megabats. There are plausible explanations for both. Let's start with the possibility that microbats evolved echolocation more than once. Echolocation is not unique to microbats: cetaceans, some cave-nesting birds, and megabats in the genus *Rousettus* use it. Within the microbats, there is considerable variation in the anatomical and physiological adaptations for echolocation and in call structure. Some of this variation is specific to particular groups, and may therefore be the result of independent origins. Similarities in echolocation systems need not imply monophyly within the microbats, but convergence due to the functional constraints of echolocation. Alternatively, could echolocation have evolved only once in ancestral bats and the megabats have subsequently lost the ability? The evolution of exceptional night vision in megabats alongside their shift to a vegetarian diet may have reduced the need for echolocation. Furthermore, echolocation may limit the maximum size of bats, since the emission of echolocation calls is coupled to the respiratory and wingbeat cycles to reduce energy costs. As bats get bigger and wingbeat frequency falls then call emission frequency also falls, reducing the rate at which the bat receives information. If megabats are going to be big, then maybe they can't echolocate. *Rousettus* is an interesting exception, since it echolocates by clicking its tongue and is probably not constrained by the wingbeat in the same way. I will come back to the evolution of echolocation in Chapter 3. Clues to this new-found relationship between megabats and rhinolophoids were there to be seen—for example, it is consistent with the exclusively Old World distribution of both groups.

I have glossed over the methods that underpin this new view of bats. Box 1.2 says a little about the complexities of phylogenetics for those who would like to know more and includes some useful references. Some of the difficulties revolve around the cladistic problems discussed earlier, but there are others unique to the molecular approach. As laboratory and analytical methods improve, molecular taxonomy becomes an ever more powerful approach and the rate at which new data are published continues to accelerate.

So, monophyly wins the day. At the height of the monophly–diphly debate Pettigrew *et al.* (1989) presented four scenarios for the relationships between microbats and megabats (the fallen angel, the deaf fruit bat, the blind cave bat, and the flying primate). For each, they suggested ways in which the situation might have arisen, and discussed the implications and difficulties of each. Only two of the four scenarios justify further discussion.

The deaf fruit bat

Megabats arose from microbats, losing the capacity for echolocation, and the associated anatomical and physiological features, and acquiring a primate-like brain in the process. Recent work has questioned the evidence for a primate-like brain (for example Ichida *et al.* 2000) and I have already suggested some reasons why the loss of echolocation may have occurred. An additional reason may be that since echolocation requires an extensive processing centre in the cortex of the brain, perhaps there is not the space for this alongside a large visual centre. However, some of the differences listed in Table 1.1 remain and require explanation: I suspect few have been fully investigated. For example, if the differences in metacarpal/phalanges indices are representative of all bats, what underlies them?

The flying primate

Microbats evolve. Megabats evolve independently on an early branch of the primate line. Is it likely that flight could have evolved twice in the mammals, and that megabats and microbats could have undergone such striking convergent evolution? As pointed out earlier, gliding has evolved many times in the vertebrates and three times in the marsupials alone (Archer 1984). Powered flight almost certainly evolved from gliding in all living and extinct animals (see Chapter 2), so its independent origin in microbats and megabats is a reasonable possibility.

Box 1.2 Phylogenetics

The principles:

1. To identify homologous DNA sequences in a group of animals. That is, identify the DNA sequence or gene responsible for producing a particular protein, which has essentially the same function in all of the organisms under study. More recently, analyses have been carried out based on non-coding homologous sections of DNA.
2. Determine the nucleotide sequences of these homologues. The greater the number of differences between sequences (due to base substitution, insertion, or deletion), the more distantly related the organisms will be.
3. Determine which is the ancestral form, and the paths by which each derived form evolved. In other words, construct an evolutionary tree, usually by cladistic analysis.

The most common analysis methods involve maximum parsimony and maximum likelihood approaches and these and a variety of other methods (for example distance matrix, Quartet, Bayesian inference) can be accessed with varying degrees of user-friendliness in a range of software packages, many freely downloadable from the Internet. Joe Felsenstein at the University of Washington, Seattle, a research leader in this field, maintains a comprehensive and up-to-date website of available programs (*http://evolution.genetics.washington. edu/phylip/software.html*). It is common practice to use several approaches and several programs in a single study, with additional programs often being used in data preparation, assumption testing, and so on. The ready availability of these programs has been a major factor in the growth of this field. Programs are constantly evaluated by the research community and improved, and new methods and programs are made available at frequent intervals. Any attempt to explain the theory behind even one or two of them would require a large box, so if you want to know more try the following references: Avise (2004, 2006), Felsenstein (2004), and Page and Holmes (1998).

Molecular taxonomy has a major advantage over many morphological methods: the degree of difference between homologues can be quantified in terms of the differences in their nucleotide sequences. Morphology is a complex and poorly understood expression of these molecular differences that cannot be readily quantified. As is usually the case in biology, there are a number of flies in the DNA soup. Some of the most important difficulties relate to the identification of homologous DNA sequences—the crucial first step in the process. Fortunately, pitfalls are increasingly easy to avoid as the genomes of a growing number of organisms are progressively mapped and made public.

Different genes appear to undergo mutations at different, but remarkably constant, rates. Functionally important DNA changes slowly: any deleterious mutations, which impair the function of its protein products, will be eliminated by natural selection. Introns mutate more rapidly, and in homologous DNA sequences show greater differences between species than their functional exons. This may complicate things for the evolutionary biologist, but it also provides a powerful tool—molecular clocks to measure the time course of evolution itself—assuming each clock can be calibrated. So, it is not only possible to identify evolutionary branch points, but also the lengths of individual branches, as shown for example in Fig. 1.5.

What about the similarity of form? Given a five-fingered mammalian forelimb, just how many ways could it develop into an aerodynamically functional wing? Probably not many, and there are a number of well-known and striking examples of convergent evolution to lend credibility to the idea: the eyes of vertebrates and cephalopods, the gills of fish and cephalopods, and the hydrodynamically efficient body form of fast pelagic swimmers among cetacea, teleost fish, and sharks. However, an overwhelming body of molecular and morphological data rejects this hypothesis.

Many of the assumptions underlying Pettigrew's hypotheses have been questioned from the start (Baker *et al*. 1991, Simmons *et al*. 1991), but the debate has been interesting and exciting. Even though the flying primate hypothesis has proved to be wrong, as Pettigrew (1991b) himself said 'it will still have been a most fruitful, wrong hypothesis'. It has raised interesting questions, prompted new research, unlikely collaborations, the application of new techniques to the study of bats, and made us question long-held beliefs. That is what keeps research buzzing.

Classification and the distribution and diversity of bats

A brief tour of modern bat families

Bats are the most widely distributed and (by species) the second most numerous group of mammals, outnumbered only by the rodents (almost 2,300 species). Precisely how many species of bats there are in the world is uncertain. The uncertainty is due in part to the difficulties of defining a species: when does a sub-species become a new species, and so on? What is certain is that the number of species is increasing, through the recognition of cryptic species within known species using molecular approaches, and through the discovery of distinctly new bats. When writing the earlier version of this book 15 years ago all sources suggested there were fewer than 1,000 species (for example Hill and Smith (1984) suggested 966 and Findley (1993) opted for 963 species). The current tally is 1,116 (Wilson and Reeder 2005), but that does not include new species that I may well mention before the end of the book. Bats therefore account for 20 per cent of the approximately 5,420 species of mammals.

Before taking a more detailed look at bat phylogeny, let's look at the global distribution of bats. Among mammals, only humans (and some of the mammals closely associated with humans) are more widely distributed than bats. Bats are found everywhere except the highest latitudes, the most inhospitable deserts, and the most remote islands. In common with all other forms of life, the number of species declines away from the equator, although the pattern is disturbed by geographical features such as the Sahara Desert. The approximate numbers of species in different regions of the globe are shown in Fig. 1.13. The neotropics of South and Central America is the richest area, with over 200 species, followed by the palaeotropical regions of Asia and then Africa. Temperate regions are impoverished by comparison, with about 40 species in North America (nearctic) and 85 or so in northern Eurasia (palaearctic). A number of species of the family Vespertilionidae spend the summer in high latitudes in both hemispheres, and a few are found north of the Arctic Circle. The Old World fruit bats have island-hopped halfway across the Pacific from the western rim, and on some islands rare, endemic
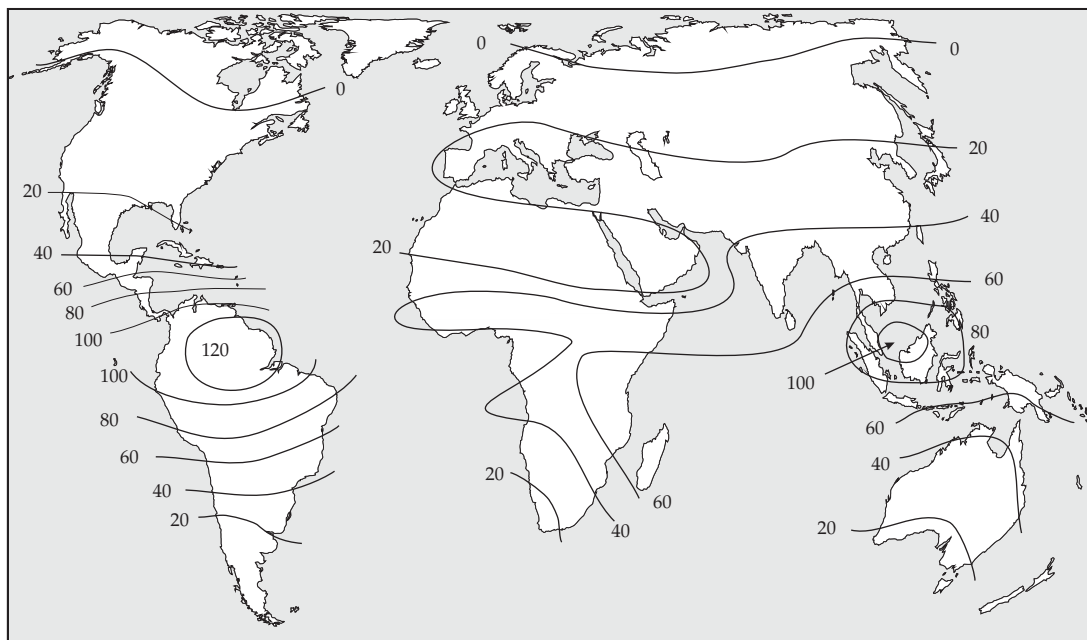

Figure 1.13 The number of bat species in 500 km² quadrats in different parts of the world. (Based on Findley 1993.)