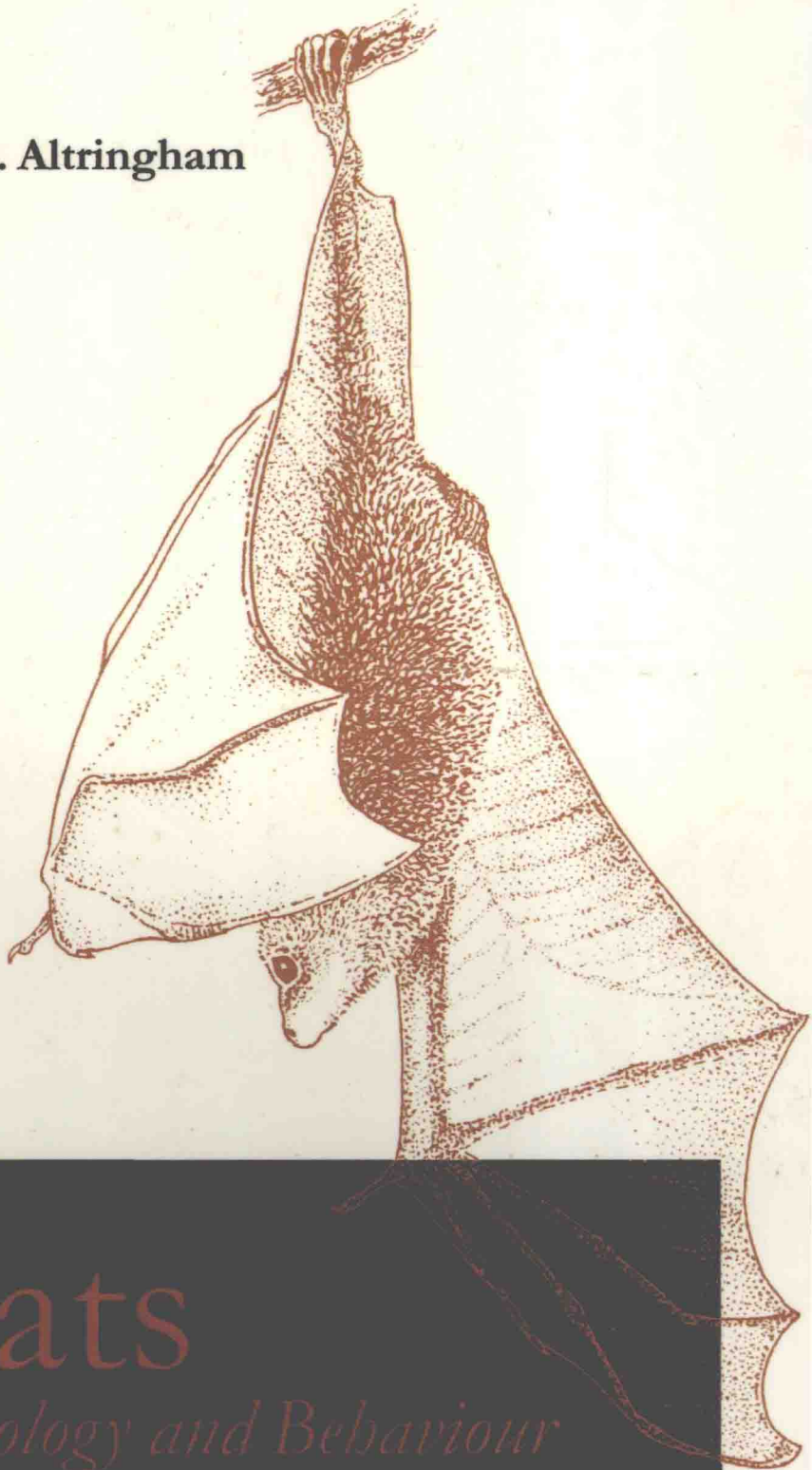


John D. Altringham



Bats

Biology and Behaviour

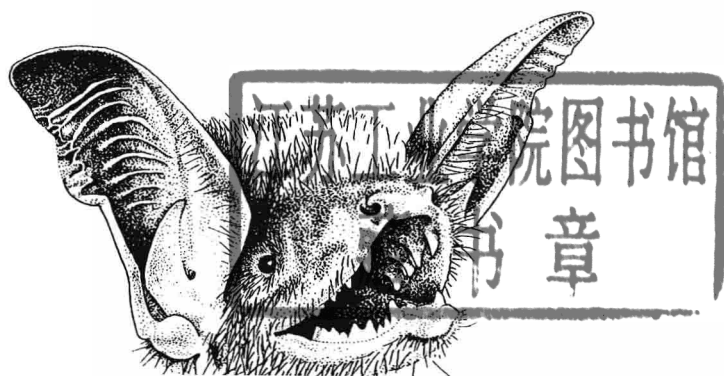
BATS

Biology and Behaviour

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The University of Leeds*

Drawings by Tom McOwat and Lucy Hammond



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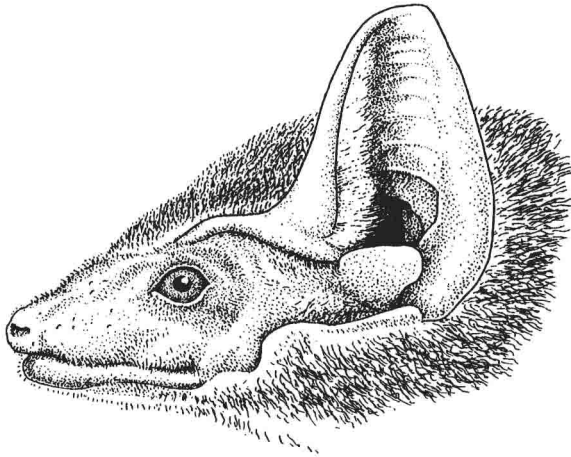
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Preface

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 which 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, emphasising those aspects which 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.



Taphozous mauritanicus

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Kate, for her understanding and support during the many hours I worked on this book, and our kids, Sandy and Anne, for only once (at least that I remember) saying 'you're not going upstairs to write that book AGAIN are you dad?'

CREDITS

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Drawings on pages iii, 30, 31, 40 (top), 43, and 44 (top) by Lucy Hammond, all others by Tom McOwat.

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Introduction—biology lessons from the bats

Bats are one of the most successful mammalian orders, and probably the most diverse. The 966 species (by the more optimistic estimates) 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, co-evolution, reciprocal altruism, the consequences of continental drift, and the arms race between predator and prey, to name just a few examples. This is a book about bats, but it will also use them as a vehicle to show how these processes shape the natural world.

Rodents are the only mammalian order to outnumber bats with, by some estimates, about 1700 species, but they are certainly less diverse in their biology. One quarter of all mammals are bats—surprising, when you think that there are 21 mammalian orders, including animals as varied as primates, carnivores, cetaceans, rodents, insectivores, ungulates, seals, sloths, marsupials, etc. They 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 (e.g. *Eptesicus* and *Lasiurus* and *Myotis* spp.) spend the summer north of the Arctic Circle. Other members of this very large family (e.g. *Dasypterus* spp.) 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 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 microbats, which may go as far back as 70–100 million years—the microbats may have watched the demise of the dinosaurs in the mass extinction at the end of the Cretaceous.

Bats range in size from the smallest mammal (the bumblebee bat, *Craseonycteris thongyai*, 1.5–2 g) to 1 kg flying foxes (*Pteropus* spp.) with wingspans of over 1.5 m. They also come in a wide range of shapes and colours. Most bats are admittedly rather drab in colour, 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—one of the best documented examples of lekking in mammals—but more are now being found among bats. The noseleaves and varied facial protuberances of many bat families are often useful identification features. Some appear to have a functional role in echolocation, e.g. 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 is unfolding around the very origins of bats. There are two sub-orders, the Old World, Megachiroptera or flying foxes, and the more widespread, more numerous, and more diverse Microchiroptera. The traditional and widely accepted view has been 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, has been compiled over the last decade. The traditional viewpoint seemed to be shaking on its weak, and largely anatomical, foundations. But new evidence for the common origin of bats is emerging from the laboratories of molecular biologists and anatomists, and the controversy becomes more finely balanced and even more exciting. The resolution of this issue, and the arguments surrounding it, are important to all evolutionary biologists, not just those interested in bats. Some basic assumptions about evolutionary processes, and the methods used to study the inter-relationships between animals, are under the microscope.

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. New theories on the aerodynamics of flapping flight have stimulated studies of the relationship between wing morphology, flight characteristics, and feeding ecology. Add to flight the ability to locate prey in the dark, and often to catch it on the wing, 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 are uncovering dazzling feats—such as the ability of greater horseshoe bats (*Rhinolophus ferrumequinum*), at least under laboratory conditions, to identify prey species from the modulated echoes returned by flying insects. Like flight characteristics, the type of echolocation used is determined by environment and the prey sought. Some bats have rather stereotyped patterns of echolocation pulses, others such as the Mexican free-tailed bat (*Tadarida brasiliensis*) have a large and plastic repertoire which gives them considerable foraging flexibility. Broad-based taxonomic evidence, and a cladistic analysis of echolocation pulse patterns, indicate a more recent evolution for the echolocating strategy of bats such as *Tadarida*.

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—much studied, but still poorly understood.

Few potential roost sites have been overlooked by bats. Mexican free-tailed bats (*Tadarida brasiliensis*) in Central America and the southern United States form cave dwelling colonies of over 20 million 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* spp.), 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

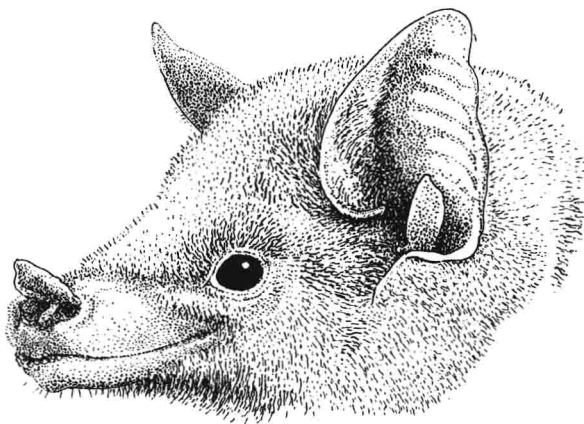
this unusual way of life include tough wings, which can be tucked away in pouches on the body, and strong talons on the thumb and toes. Several species (e.g. *Artibeus*, *Ectophylla*, and *Uroderma*) bite through the main supporting ribs of palm and *Heliconia* leaves to collapse them into tents, and in Gabon, *Myotis bocagei* roosts inside the flowers of the water arum. Two species of *Tylonycteris* 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 (which roost in furled leaves) the Myzopoda of Madagascar, and the Thyroptera of Central and South America—another example of related species separated by the fragmentation of Gondwanaland, or of convergent evolution? The availability of some of the more unusual roosts may be a factor limiting the density and distribution of certain bats.

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, and of course blood. Many are highly specialised in their diets, but others, e.g. some 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 of many interesting and informative investigations. Evidence for optimal foraging in the feeding strategies of animals is constantly being sought. One excellent mammalian example involves the Mexican long-nosed bat, *Leptonycteris curasoae* (*sanborni*), which feeds primarily on the saguaro cactus (*Carnegiea*) and the tequila agave (*Agave*). Careful field observations, outdoor experiments with glass flowers, and computer models, together suggest that the flock feeding behaviour of these bats is governed by a set of simple rules, which work to maximise energy intake. Very new work is uncovering possible examples of optimal foraging among insectivorous bats. Nectar and fruit eating bats also provide the biologist with some fascinating examples of co-evolution. Take, for example, the relationship between the tree *Oroxylum iridicum* and a small pteropodid, *Eonycteris spelaea*. The flowers of *Oroxylum* open 2.5 hours after dark—when the bats first reach them from their distant roosts. In the meantime, no other species can get in. The flowers fall before dawn. *Eonycteris* is just the right size to put its head in the flower, just the right weight to tip the flower and load a tuft of hairs with nectar, and has a tongue just the right length to reach the nectar. The flower releases just enough nectar to persuade the bat to move on to the next flower—and the next—maximising the chances of pollination.

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 arms race is perhaps 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 which are less audible to moths, or catch them without using echolocation. Incidentally, noctuids were about almost 70 million years ago, further indirect evidence for the very early evolution of microbats—in the absence of echolocating bats, noctuids would not need ears.

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 the 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 spear-nosed bats) are the family to go to for a lesson in adaptive radiation. The family contains about 147 species in 51 genera. They are fewer and far less widespread than the Vespertilionidae or evening bats, but are unmatched in their range of foods. 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 3 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 tent-makers, the record-breaking kidneys of vampires, and the chin-flap-cum-night-cap of the wrinkle-faced bat. The Phyllostomidae are a taxonomic hotbed, and controversial new classification schemes are published at intervals creating a lively and thought provoking scientific debate. My hope is that this book will be a thought provoking biology lesson from the bats, a group about which we know remarkably little compared with many other mammals, but which has already given us some rewarding insights of broad biological significance.



Leptonycteris curasoae

1 The evolution and diversity of bats

Fossil bats—the evolutionary history of bats. The origins of flight and echolocation (covered in detail in later chapters). Megabats and microbats—a common ancestor or a stunning example of convergent evolution? The current controversy over the origin of bats, the methods being applied to the problem and their wider significance. A brief classification of modern bats. The sub-orders: mega- and micro-bats. Brief descriptions at family level. The Phyllostomidae—an example of adaptive radiation.

EVOLUTION

Fossil bats

Bats are currently placed in a single order, the Chiroptera. They are divided into two sub-orders, the Mega- and Microchiroptera, commonly referred to as the megabats and microbats. The megabats are the Old World fruit bats: large (for bats, 20–1500 g), exclusively plant-eating (i.e. they eat fruit, flowers, nectar, and pollen), and confined to Africa, tropical Asia, and Indo-Australasia. There are about 175 living species, all belonging to one family, the Pteropodidae. Microbats on the other hand are found on every continent except Antarctica, and on many isolated islands. They are, as their name implies, generally smaller than megabats (1.5–150 g), and they eat all sorts of things, as we'll discover later, although the ancestral microbat almost certainly ate insects and other arthropods. The approximately 790 species are distributed among 17 families. Figure 1.1 will fulfil our immediate needs as we look at the origins of bats, and the source of this diversity. It shows the known fossil bats in relation to a simplified evolutionary tree of extant bats.

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. A decade ago, fossils of 132 species had been found: 92 of extant species, 40 extinct. The 40 extinct species are distributed through 30 genera and 11 families, and 8 living species are known for 8 of these families (Hill and Smith, 1984). The ratio of known extinct to living species is low for bats, in relation to other mammals, so the big question is whether this fossil record can provide some clues to the origins of bats. Recent, exciting discoveries in Australia of an extensive fossil bat fauna, dating back 55 million years, may prove to be very important.

The origins of microbats

What do the earliest fossils tell us about microbat evolution? The answer is, surprisingly little. The oldest fossil bat, *Icaronycteris index*, was found in the Polecat Bench formation

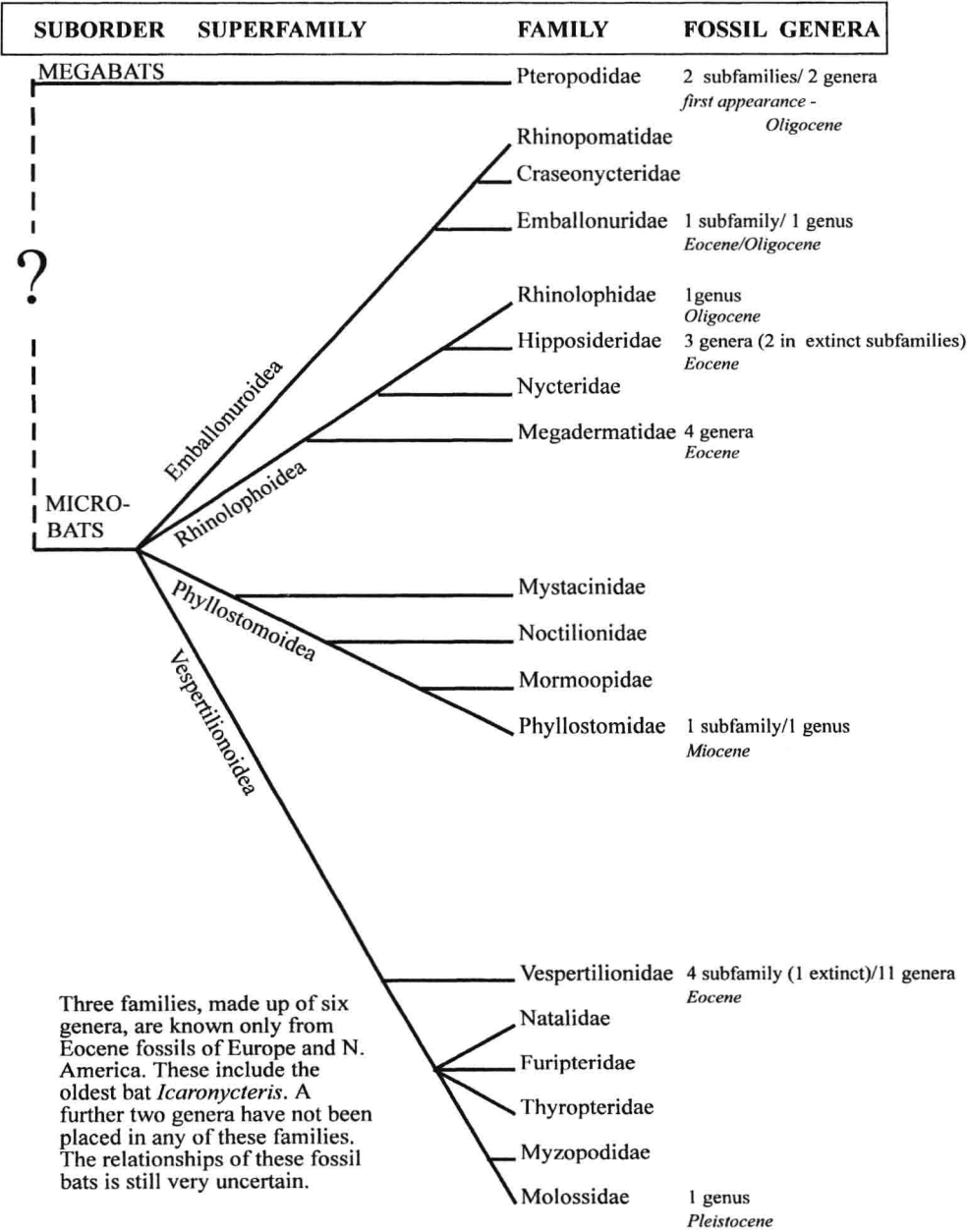


Fig. 1.1. An evolutionary tree of modern and fossil bats.

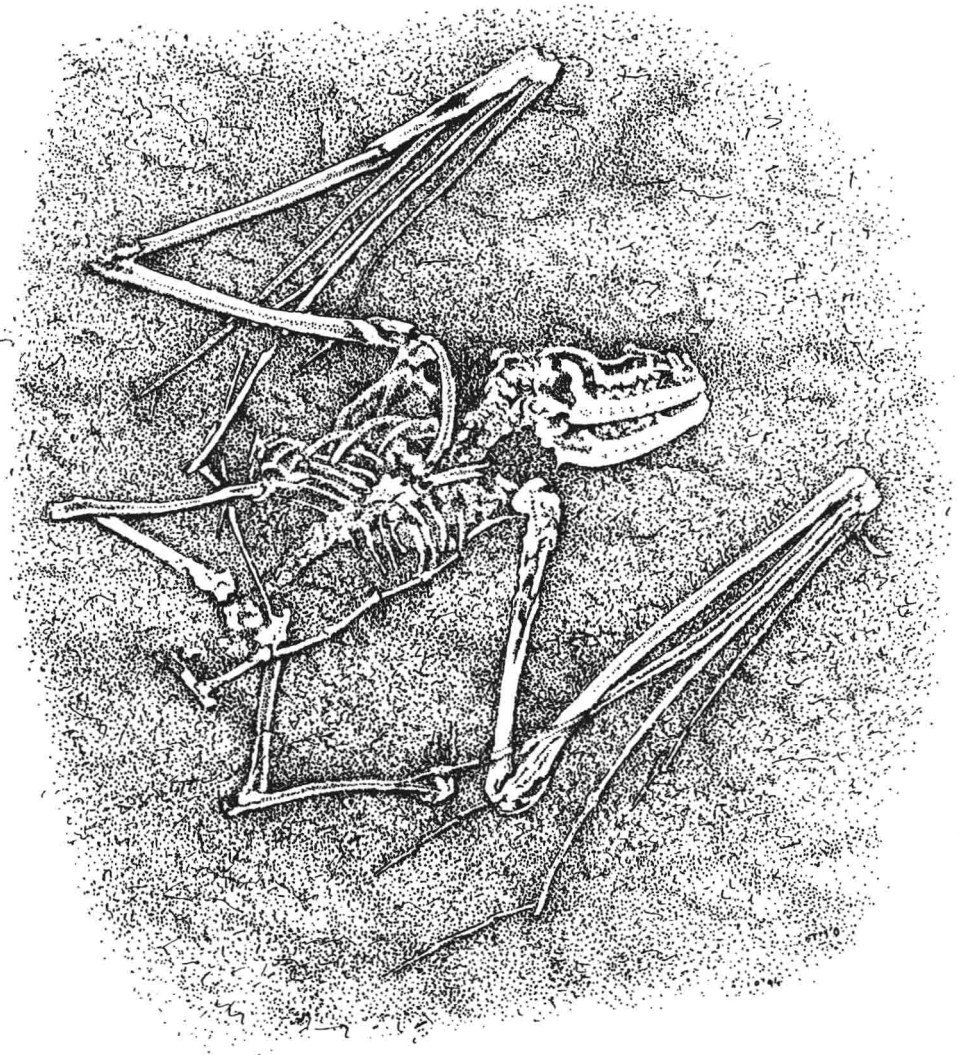


Fig. 1.2. *Palaeochiropteryx tupaiondon*, an Eocene fossil bat from Messel in Germany.

of Wyoming, not far from Yellowstone Park in the United States, and has been dated to the early Eocene, 50 million years before the present (myr BP) (Jepson, 1966; 1970). *Icaronycteris* looks remarkably like a modern microbat. 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 so good that recognisable insect remains can be seen in the gut of some specimens. All date back about 45 million years, and all resemble modern microbats. A lavishly illustrated book has recently been published on the Messel beds, with superb photographs of these bats (Schaal and Zeigler, 1992). No fossil bats are known

which are in any way intermediate in form between a modern microbat and some early tree-living ancestor which might have got around by jumping or gliding. Figure 1.3 shows the first appearance of bats in relation to some other mammals. Most mammalian groups began their big radiation (i.e. a dramatic increase in the number of species) around 50 myr BP, and bats are probably no exception.

If we allow time for the evolution of these sophisticated aerial insectivores, with an apparently advanced echolocating capability, then microbats may have made their appearance 65–100 M years ago, in the early Palaeocene (65–53 myr BP) or late Cretaceous (135–65 myr BP). 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? There is little evidence of real substance, but some of a persuasive, if circumstantial, nature. As we'll see a little later, microbats show no close affinities to any other mammalian order: the nearest, but still distant order, may be the Edentates—anteaters and sloths, themselves a very ancient group. These are unlikely ancestors for the bats, and they probably evolved from something similar to modern tree shrews. This inability to link bats to any known mammalian group in itself suggests a very early origin. 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 fossilised egg of a noctuid moth in deposits at Martha's Vineyard in Massachusetts which date back to about 75 myr BP. All known living and extinct noctuids are tympanate, and their ears are tuned to the ultrasonic frequency range used by many bats. If the moth that laid this egg was tympanate, then echolocating bats may already have been around for a while 75 million years ago. Finally, there are a number of cases where possibly closely related microbat species live on once adjacent, but now distant, fragments of Gondwanaland, the supercontinent which broke up into the fragments which now make up the land masses of the southern hemisphere. This process

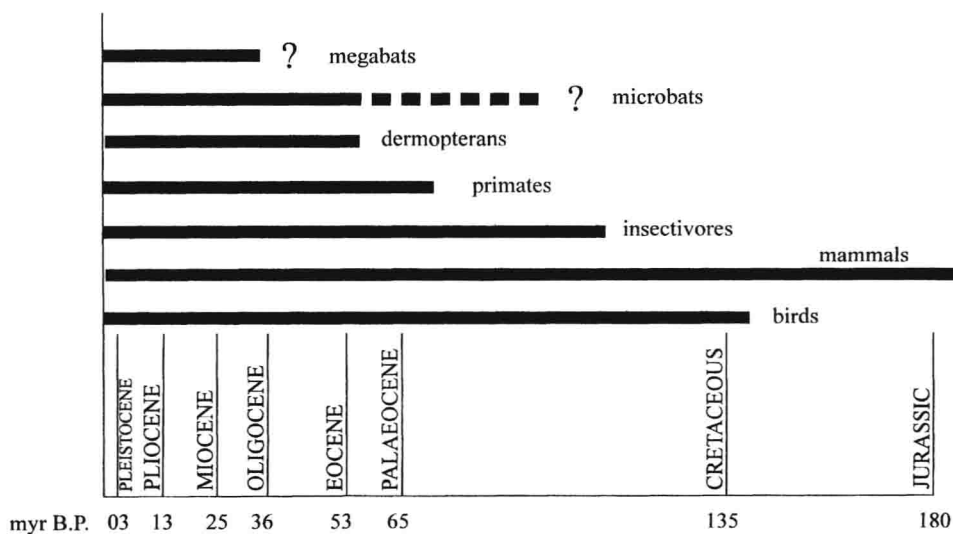


Fig. 1.3. A proposed time scale for the evolution of bats and other mammals.

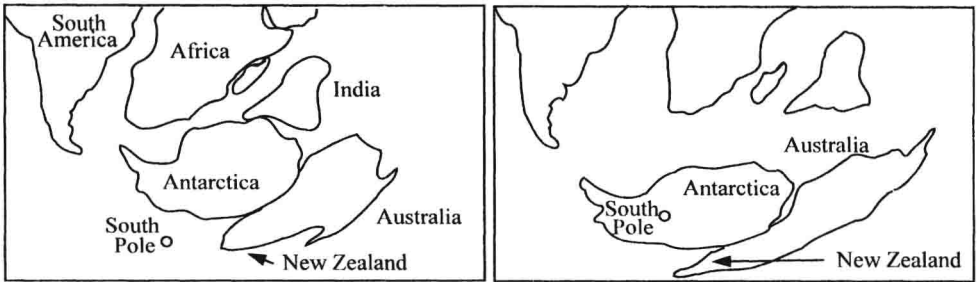


Fig. 1.4. The break-up of Gondwanaland. The fragments in the early (left) and late (right) Cretaceous. New Zealand broke away from the Australian plate shortly after the end of the Cretaceous.

went on right through the Cretaceous, starting with the separation of Antarctica/Australasia from South America, and ending with the separation of Australia from Antarctica around 50 million years ago (Fig. 1.4).

New Zealand has just two endemic mammalian species, both bats. The closest living relatives of the short-tailed bat (*Mystacina tuberculata*) are the fisherman bats (*Noctilio*) of South America (Pierson *et al.*, 1986). The link is based on an immunological comparison of the proteins albumin and transferrin, supplemented by a number of morphological similarities. The ancestors of these bats either separated as much as 80 million years ago, when New Zealand drifted away from the Antarctic–Australian Plate, which connected it ultimately to South America (Griffiths and Varne, 1972), or an ancestral *Mystacina* somehow made the long journey to New Zealand via Antarctica with long ocean stretches. Pierson *et al.*, assuming that bats originated in the Palaeocene, 55–65 myr BP, suggest the separation occurred around 35 million years ago, but they confess to uncertainty about the speed of the molecular clock on which they base their estimate. On the basis of the unusual suckers on their wrists and ankles, and a number of skeletal characteristics Yalden and Morris (1975) suggest that the Myzopoda from Madagascar, and Thyroptera from South America may be related. Is this another case of related species isolated by the break up of Gondwanaland, as Pettigrew *et al.* (1989) propose, or an example of convergent evolution? Pettigrew and colleagues also argue that all of the more primitive microbats are restricted to fragments of Gondwanaland. The recently discovered bumblebee bat, *Craseonycteris thonglongyai* (Hill, 1974), at first appears to be something of a puzzle, in that it is primitive, but restricted to a tiny area of western Thailand. However, this spot happens to be part of the Indo-Australian plate, and one of a number of small limestone fragments of Gondwanaland in South East Asia (Audley-Charles, 1983).

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 myr BP), and modern