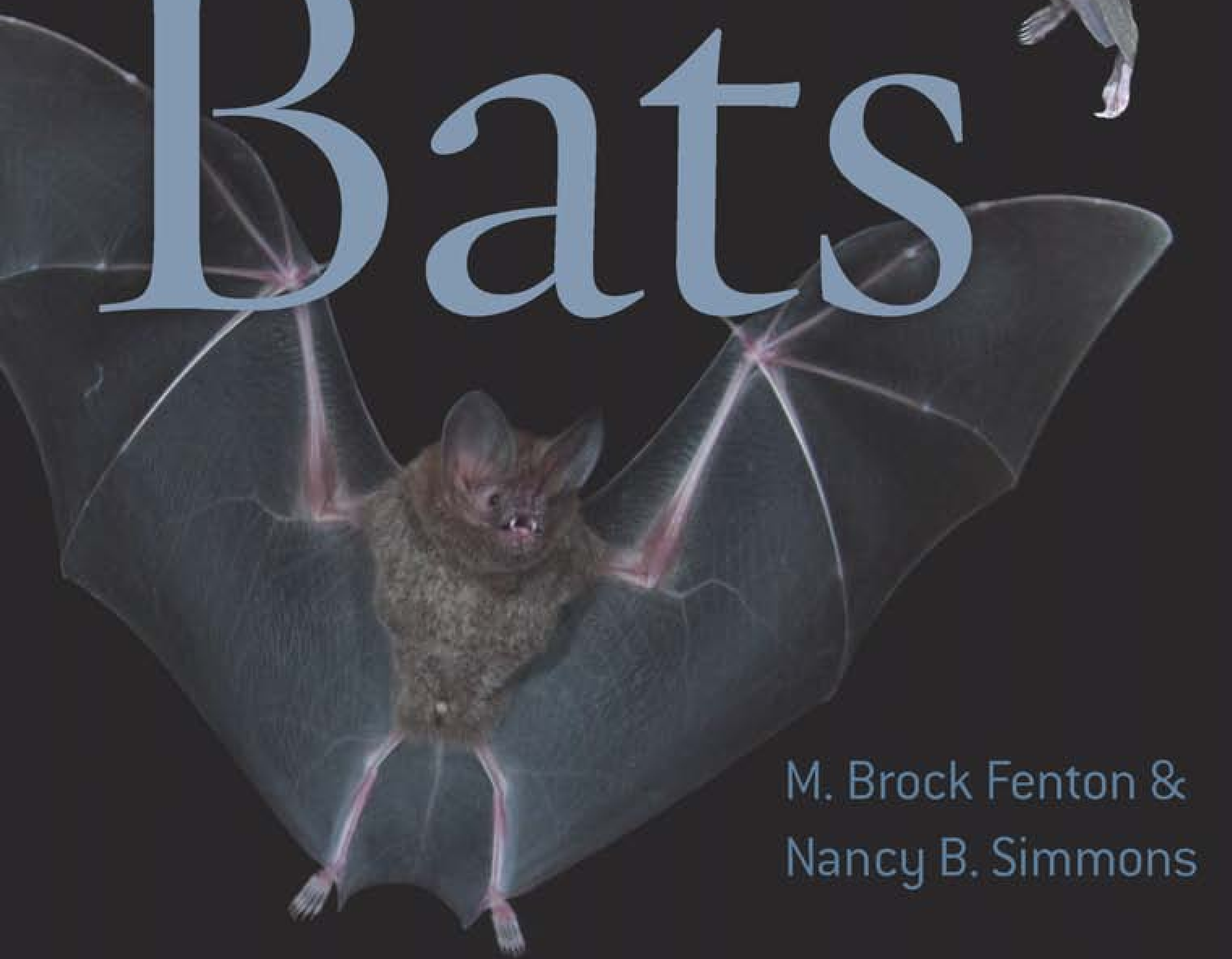
A WORLD
OF SCIENCE
AND
MYSTERY

Bats



M. Brock Fenton &
Nancy B. Simmons

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A World of Science and Mystery

M. Brock Fenton
Nancy B. Simmons

A Peter N. Névraumont Book

The University of Chicago Press
Chicago and London

We are pleased to dedicate this book to the memory of the late Karl F. Koopman, a pioneer in the study of bats.

M. Brock Fenton
Is emeritus professor in the Department of Biology at the University of Western Ontario. He is the author or editor of several books, including *Bat Ecology*, also published by the University of Chicago Press.

Nancy B. Simmons
Is curator-in-charge of the Department of Mammalogy at the American Museum of Natural History, where she is also professor in the Richard Gilder Graduate School.

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Contents

1

It’s a Bat!

Figure 1.1.
A flying Jamaican Fruit Bat (*Artibeus jamaicensis*) showing the wrist (**w**), thumb (**t**), forearm (**fa**), elbow (**e**), ear (**ea**), knee (**k**), hind foot (**hf**), calcar (**ca**) and tragus (**tr**).

Introduction

The most distinctive features of bats are their wings and nocturnal habits. Fossils show that bats have been around for over fifty-two million years. (See Chapter 2.) If one had a time machine and could stand on the bank of an ancient stream or lake at nightfall, the flying creatures that swooped through the skies would be immediately recognizable as bats. Then, as now, bats would have appeared as quick and mysterious animals. (Figure 1.1)

People have always wondered about bats. From the time of Aesop, there have been stories suggesting that bats are otherworldly, part mammal and part bird. In some folk stories, bats are portrayed as duplicitous because they can alternate between being birds and being mammals. A recurring story recounts a ball game between birds and mammals. In one version, bats are shunned by both sides because they appear to be a mixture of the two. In another, flight allows them to score the winning point and makes them heroes, at which point they are recognized as mammals.

BOX. 1.1

Bats are Mammals

As mammals, each of us can probably think of some key features that we share with other mammals. These could include having hair or fur, giving birth to live young and feeding them with milk and having two generations of teeth (baby or milk teeth and permanent teeth). (See Chapter 7.) Bats meet all of these criteria. The basic anatomy of bats is mammalian, from skeleton to organs. Bats' hearts tend to be larger than those of other mammals of comparable size, no doubt reflecting the demands of powered flight. Bats also have some muscles lacking in other mammals, again related to their flying lifestyle. (See page 19.)

Bats are considered warm-blooded (homoeothermic) because they maintain high body temperatures when active, as do most mammals. Many bats, however, have internal thermostats that allow their body temperature to vary with ambient temperature, a specialization thought to save energy. (See Chapter 6.) This versatile approach is known as heterothermy and is a strategy that also appears in other groups of mammals, such as rodents. Bats of temperate regions especially benefit from this approach to thermoregulation.

Bats have evolved diverse dietary habits including insectivory, carnivory, frugivory, nectarivory, piscivory (fish eating) and even sanguinarivory (blood feeding). (See Chapter 5.) In this respect bats are remarkable: no other group of mammals exhibits such ecological diversity. There are no known toothless bats although a permanent evolutionary loss of teeth has occurred in some other mammals, such as anteaters. There is no evidence that bats or their immediate ancestors laid eggs. Among modern mammals, monotremes (duck-billed platypus, spiny anteater) are the only egg-layers. Bats have a placenta that facilitates exchange of nutrients and wastes between the blood of the mother and that of the fetus. Bats and all other placental mammals give birth to well-developed young. This makes placental mammals (including bats) distinct from the pouched mammals (marsupials such as opossums, kangaroos and their relatives) that bear tiny embryos that must be nurtured attached to the mother's nipple before developing sufficiently to move around alone. There is no evidence of bat-like mammals having evolved from marsupial stock.

Names of Bats

Although bats are mammals, some of the names that humans use for bats reflect the imagined dichotomy between their mammal-like and bird-like aspects. (Box 1.1) The common French name for bat is "chauve souris" or "bald mouse." In German, it is "fledermaus" or "flying mouse." But, as Denise Tupinier pointed out in her excellent book, the French have had other names for bats, such as "souris chaude" (hot mouse), "souris volante" (flying mouse), or "pissarata" (name says it all). In Scotland, bats are sometimes known as "gaucky birds", in Norway as "flaggermaus", in Holland as "viermuis." Other names for bats refer to their nocturnal activity. For example, the Greek "nycteris" refers to night, as does the Polish "nietopyr." Names such as the English "bat" do not refer to other animals or to nocturnality, instead being a unique label for a unique animal. The word "bat" is thought to be derived from the Middle English "bakke" (early 14th century.), which is probably related to Old Swedish "natbakka", Old Danish "nathbakkæ" ("night bat") and Old Norse "leðrblaka" ("leather flapper"). It is clear that humans have almost always had special names for these mysterious flying creatures of the night.

"Common" versus "scientific" names complicate the issue of naming bats. A common name is the one by which the mythical average person knows the animal. Many will recognize the common names of animals such as birds (American Robin, Bald Eagle and Nightingale). The common names of birds are standardized and relatively consistent. This is not the case for living bats, let alone fossil ones.

Scientific names of species are Latinized binomials (two-part names) that describe the organism and its general place in the overall classification of life forms. Although scientific names of larger groups such as families are written as single words in regular fonts, *e.g.*, "Pteropodidae" for Old World Fruit Bats, scientific names of species are always presented as paired names (binomials) in italics. So, *Myotis lucifugus* is the scientific name of what many people know as the Little Brown Myotis and others as the Little Brown Bat. Every species has one unique scientific name, but it may have several common names as in the case of *Myotis lucifugus*–or none at all, for example, *Onychonycteris finneyi*, a fossil bat. Using scientific names increases the precision of communicating about bats, but these names intimidate the non-technical reader. In this book we use common names wherever possible, but the first time we refer to a bat we also provide its scientific name for clarity. Biologists are much more familiar with scientific name, but variation in pronunciations of the Greek and Latin are still a challenge for them. Nobody has asked bats what they think about "common" versus scientific names. The names of all the bats in this book, both scientific and common, can be found in Bats in the Book on page 288.

Nancy Makes Up Common Names

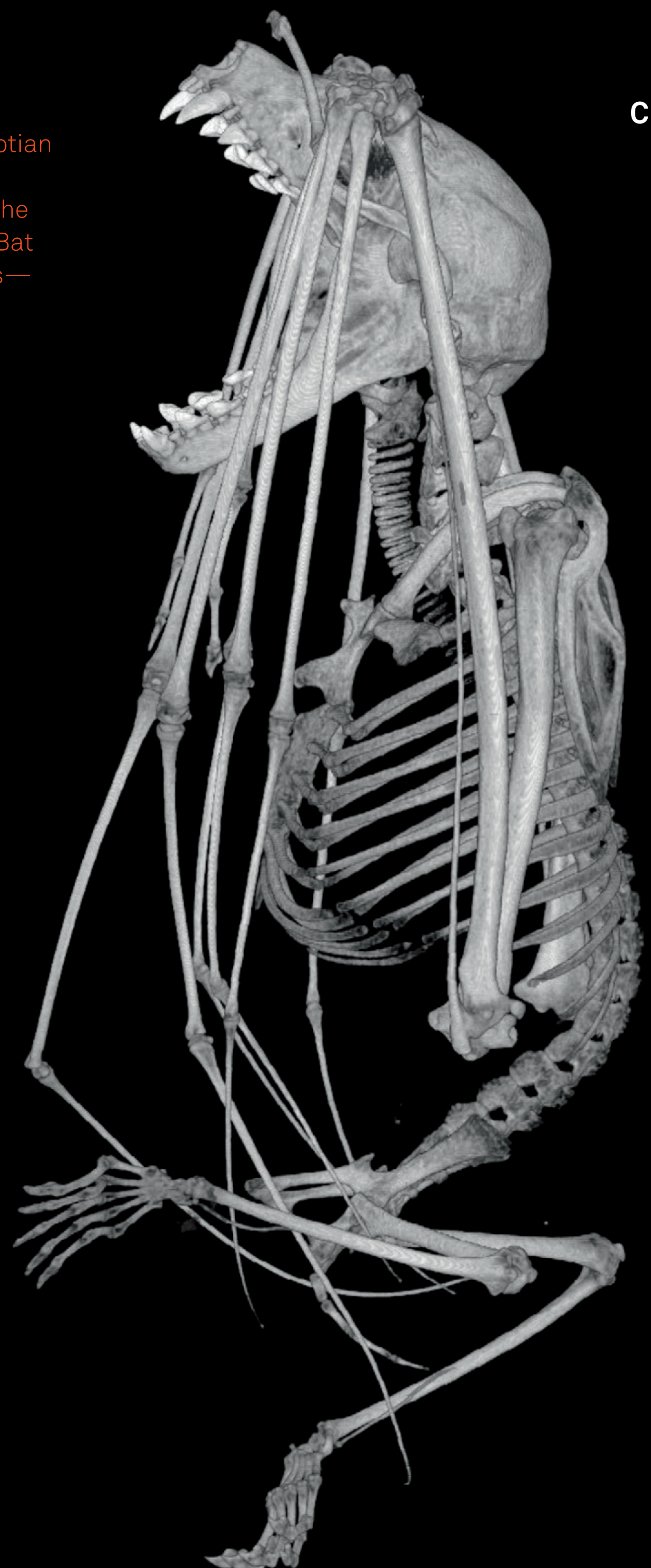
When I was finishing up writing the Chiroptera chapter for the reference book Mammal Species of the World in 2004, I found myself facing an odd problem. The editors of the book wanted to include common names for every species—yet I found that more than fifty species of bats didn't have common names. They had been described properly in the literature with unique binomial scientific names, *e.g.*, *Myotis lucifugus*, but nobody had ever used common names for them as far as I could tell. What to do? With the permission of the editors, I simply made up names for them! Most often I coined the common name for a bat using a variant of its scientific name, *e.g.*, *Micronycteris brosseti* became "Brosset's Big-eared Bat", after the scientist for whom it was named. In other cases, the geographic range of the species helped to provide a common name, *e.g.*, *Leptonycteris curasoae* became the "Curaçoan Long-nosed Bat." It was tempting to make up silly names in some cases—I really wanted to designate a species as the "Common Baseball Bat" just for fun—but I managed to resist the temptation. I have always rather regretted that!

Table 1. The diversity and distribution of modern bats. There are twenty families and >1300 species of living bats recognized today, and about ten new species are described every year. "Laryngeal" under Echolocation means that the sounds used for echolocation are produced in the larynx (voice box).

Common Name	Scientific Name	# of Species	Echolocation	Diet	Distribution
Old World Fruit Bats	Pteropodidae	198	absent or tongue clicks	fruit, flowers, leaves	Africa, Asia, Australia, Pacific Islands
Mouse-tailed Bats	Rhinopomatidae	6	laryngeal	insects	Africa, Southern Asia
Bumblebee Bats	Crasoncyteridae	1	laryngeal	insects	Southeast Asia
Horseshoe Bats	Rhinolophidae	97	laryngeal	insects	Eurasia, Africa, Southeast Asia, Australia
Old World Leaf-nosed Bats	Hipposideridae	9	laryngeal	insects	Africa, Southeast Asia, Australia
False Vampire Bats	Megadermatidae	5	laryngeal	insects, small animals	Africa, Southeast Asia, Australia
Slit-faced Bats	Nycteridae	16	laryngeal	insects, small animals	Africa, Southeast Asia
Sheath-tailed Bats	Emballonuridae	54	laryngeal	insects	Pantropical: Africa, Southeast Asia, Australia, Tropical Americas
New World Leaf-nosed Bats	Phyllostomidae	204	laryngeal	fruit, flowers leaves, insects small animals, blood	Tropical Americas, Caribbean Islands
Moustached Bats	Mormoopidae	10	laryngeal	insects	Tropical Americas, Caribbean Islands
Bulldog Bats	Noctilionidae	2	laryngeal	insects, fish	Tropical Americas, Caribbean Islands
Smoky Bats	Furipteridae	2	laryngeal	insects	Tropical Americas
New World Disk-winged Bats	Thyropteridae	5	laryngeal	insects	Tropical Americas
Old World Disk-winged Bats	Myzopodidae	2	laryngeal	insects	Madagascar
New Zealand Short-tailed Bats	Mystacinidae	2	laryngeal	insects, fruit, flowers	New Zealand
Funnel-eared Bats	Natalidae	12	laryngeal	insects	Tropical Americas
Free-tailed Bats	Molossidae	113	laryngeal	insects	Eurasia, Africa, Asia, Australia, Americas
Bent-winged Bats	Miniopteridae	29	laryngeal	insects	Eurasia, Africa, Asia, Australia
Wing-gland Bats	Cistugidae	2	laryngeal	insects	Southern Africa
Vesper Bats	Vespertilionidae	455	laryngeal	insects, fish	Worldwide except Arctic & Antarctica


A
B

Figure 1.2.
The hand wing of bats. In **A** the wings of a flying Egyptian Rousette Bat clearly show the basic hand structure which also is obvious in **B**, the skeletal structure of the hand wing. A CT scan of a Lesser Short-nosed Fruit Bat (*Cynopterus brachyotis*) reveals the size of the wings—even when folded—with respect to the rest of the skeleton. (See also Figures 2.1, and 2.2.) CT scan (**C**) courtesy of Nancy Simmons.

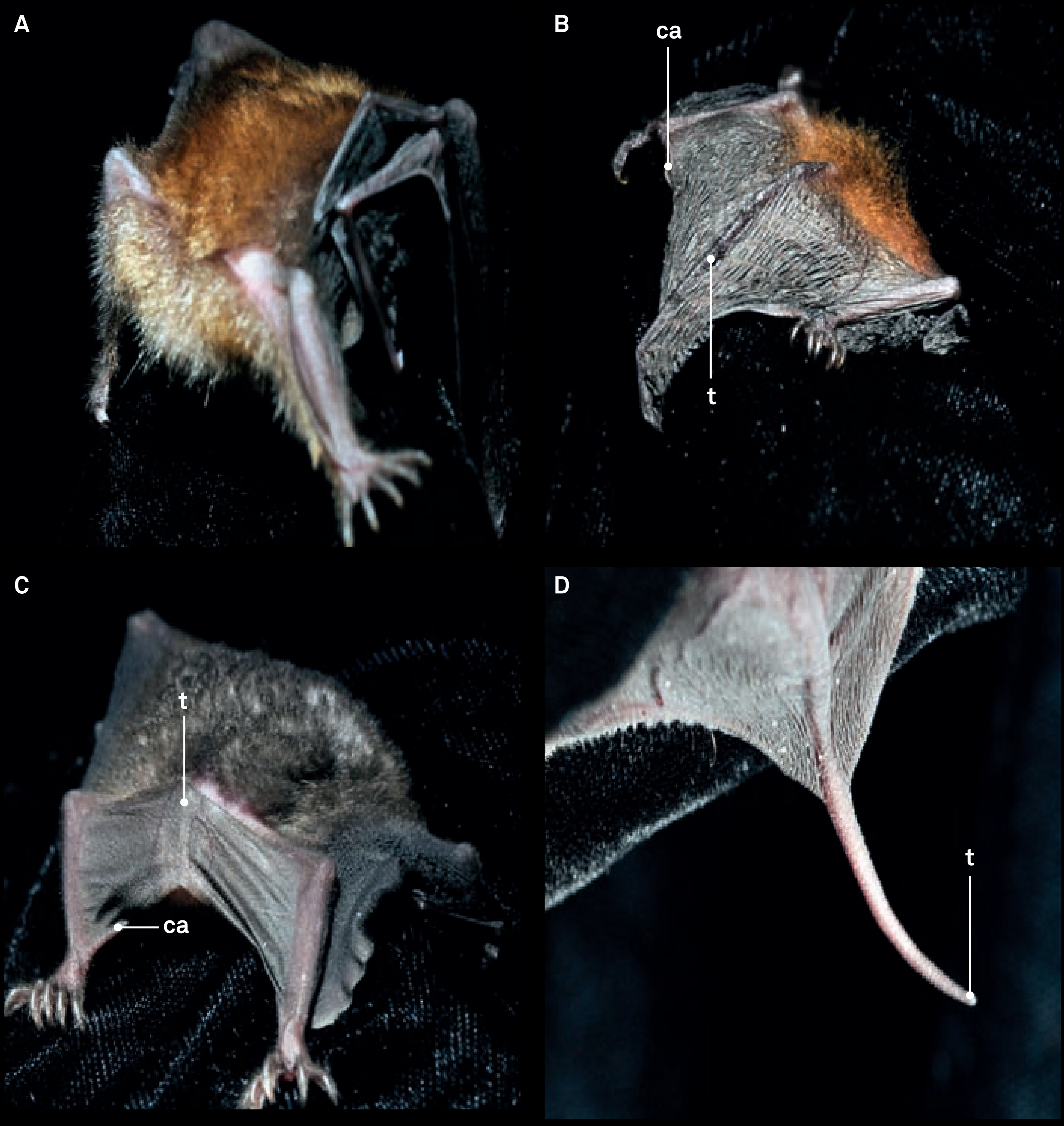


Bats constitute the order Chiroptera, from the Greek *cheiro* meaning hand, and *ptera* meaning wing. (Figure 1.2) They are the second largest group of mammals after rodents, representing about 20 percent of all classified mammal species worldwide. The >1300 species of living bats are arranged in twenty families based on their morphology, DNA and evolutionary history. Each family of bats has a scientific and at least one common name as shown in Table 1. Bats are currently classified in two suborders, the Yinpterochiroptera (yinpterochiropterans) and the Yangochiroptera (yangochiropterans). In the past scientists divided bats differently, recognizing groups called Megachiroptera (megabats = Old World Fruit Bats) and Microchiroptera (microbats = echolocating bats). These terms are no longer in use because evolutionary studies of DNA have shown that some "microbats" are actually more closely related to Old World Fruit bats than they are to other echolocating bats. Also, these terms were always misleading in the first place because some "mega-bats" are quite small, *e.g.*, Long-tongued Fruit Bats (*Macroglossus minimus*) have a wingspan of 15 centimeters (cm.) and weigh only 12 to 18 grams (10 grams = 0.35 ounces), while some "microbats" are quite large, *e.g.*, Spectral Bats (*Vampyrum spectrum*) can have wingspans of about 1 meter (m.) and weigh nearly 200 grams (g.). Also, at least two "megabats" echolocate using tongue clicks—the Egyptian Rousette (*Rousettus aegyptiacus*) and Geoffroy's Rousette (*Rousettus amplexicaudatus*)—making the distinctions even more confusing. Regardless, most scientists now use tongue-twisting names Yinpterochirotpera and Yangochiroptera—derived from "yin" and "yang" in Chinese philosophy—to describe the two main groups of bats. The geographic range of families of bats in each group is shown in Table 1.

Map to a Bat

Many of a bat's distinctive features are obvious when the animal is flying (Figures 1.1 and 1.2), but when a bat is roosting, other features become more obvious. (Figure 1.3) We have labeled some of the relatively consistent features in these figures to make them easier to interpret. All bats have two wings with flight membranes (called patagia, singular = patagium), as well as two hind legs with feet. Some bats have a membrane between the legs (uropatagium or interfemoral membrane) but others do not. Bats often have calcars, cartilaginous or bony projections from the ankle towards the tail, which allow control of the shape and stretch of the interfemoral membrane. (Figure 1.3) Tail length varies considerably in bats, spanning the whole range seen in other mammals—from very long to nonexistent.

Figure 1.3.
Three roosting bats with wings that are fully folded (**A**, **C**), or partly folded (**B**). The Lesser Mouse-tailed Bat (*Rhinopoma hardwickei*) shown in (**A**) has an obvious and distinct tail; its feet and thumbs are also clearly visible. (**B**) The Honduran White Bat (*Ectophylla alba*) hangs by one foot. Its feet are obvious. (**C**) The Lesser Short-nosed Fruit Bat (*Cynopterus brachyotis*) partly envelops its body with its wings.



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D
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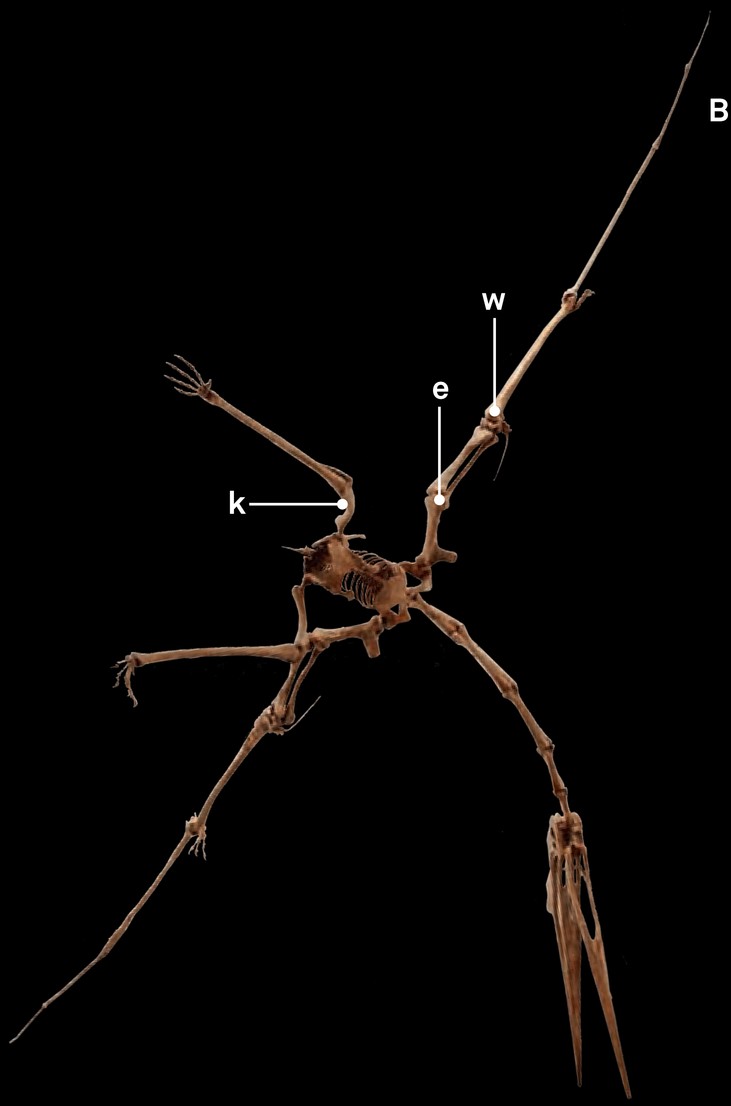
Similar Yet Different: Bats Compared to Birds and Pterosaurs

The wing skeletons of bats and those of other flying vertebrates—birds and pterosaurs—are very different from one another although they originated evolutionarily from the same basic set of arm bones common to all terrestrial vertebrates. (Figure 1.5) Ancestrally, the arm skeleton of bird, bat and pterosaur precursors contained the same set of bones that humans have: a single upper arm bone (humerus), a pair of forearm bones (radius and ulna), a group of small bones comprising the wrist (carpals), five hand bones (metacarpals) and five digits each consisting of two to three finger bones (phalanges). The arm and hand skeleton of each flying group evolved to include elongation of different parts of the arm and hand and fusion of different bones to support a wing membrane or airfoil. Note the differences in the positions of elbows and wrists between bats and pterosaurs. The humeri (upper arm bones) of pterosaurs and birds are proportionally much shorter than those of bats. In bats the wing membrane is supported by elongated arm bones (especially those of the forearm) and elongate hand and finger bones in four digits; only the thumb in bats remains relatively small. Pterosaurs, by comparison, had flight membranes supported by a single elongated hand and finger bone. (See following page.)

Figure 1.4. (opposite)
Tails of bats. (**A**) Little Yellow-shouldered Bat (*Sturnira lilium*), a tailless species, (**B**) long tailed Elegant Myotis (*Myotis elegans*), (**C**) Sowell's Short-tailed Fruit Bat (*Carollia sowellii*) and (**D**) Brazilian Free-tailed Bat (*Tadarida brasiliensis*). Arrows point to tails (**t**) and calcars (**ca**). Note the tail in Figure 1.3A.

A

Figure 1.5.
A comparison of (**A**) the skeleton of a Flying Fox and (**B**) a reconstruction of the skeleton of a pterosaur, *Quetzalcoatlus northropi*, as well as (**C**) the wing bones of a bird. The prominent wings of bats and pterosaurs are clear. Arrows show elbows (**e**), wrists (**w**) and knees (**k**). The bird's bones show the points of anchorage of flight feathers.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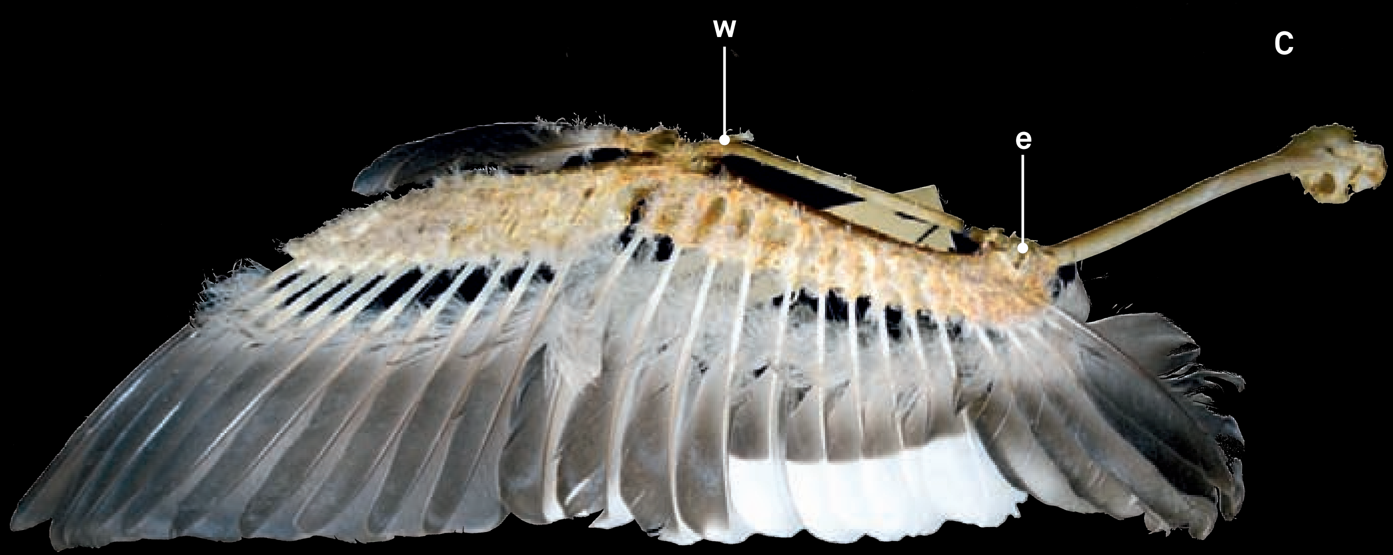
e
k


w
C
e

Pterosaurs may have had wing membranes made of skin like those of bats, but exceptionally well-preserved fossils of pterosaurs from China and elsewhere show that pterosaur wing membranes were filled with parallel fibers arranged perpendicular to the bone of the wing digit. Bat wings have many elastic strips and muscles in their wing membranes, but only some of them are arranged perpendicular to the arm or finger bones. (Figure 1.6)

The precise structure and function of the fibers in pterosaur wings remain a mystery, but doubtless these structures were important for wing function during flight. In birds, feathers comprise the flight surface and the bones of the wrist and hand have become fused to provide a robust attachment site for flight feathers. The fact that three different vertebrate groups achieved powered flight using modified forearms to produce an airfoil (the shape of the wing seen cross-section)—but did so in entirely different ways—is an excellent example of parallel evolution. (See Chapter 3.)

There are other striking differences between bats and birds in addition to their wing structure. In birds that fly, the breastbone (sternum) has a conspicuous keel, while bats typically have only a small keel that is often limited to very anterior end of the breastbone. (Figure 1.7) Birds have a wishbone (furculum) composed of fused collar bones (clavicles), whereas the clavicles in bats remain separate. Special flanges called uncinate processes produce overlap between the ribs of birds and reptiles, but these are not present in bats (or other mammals). The diaphragm and movements of the ribs are important during breathing in mammals. The absence of uncinate processes is correlated with a more flexible chest skeleton in mammals. The lungs of birds are open at either end, allowing air to flow through and resulting in more efficient breathing and cooling. Bat lungs, like our own, are dead-end sacs that cannot be as effectively ventilated as bird lungs. But the blood-gas barrier in the lungs of bats is thinner than that of other mammals, the alveoli are smaller and the lungs proportionally larger than those of mammals that do not fly. Finally, modern birds lack teeth and lay eggs, but all known species of bats have teeth and bear live young.

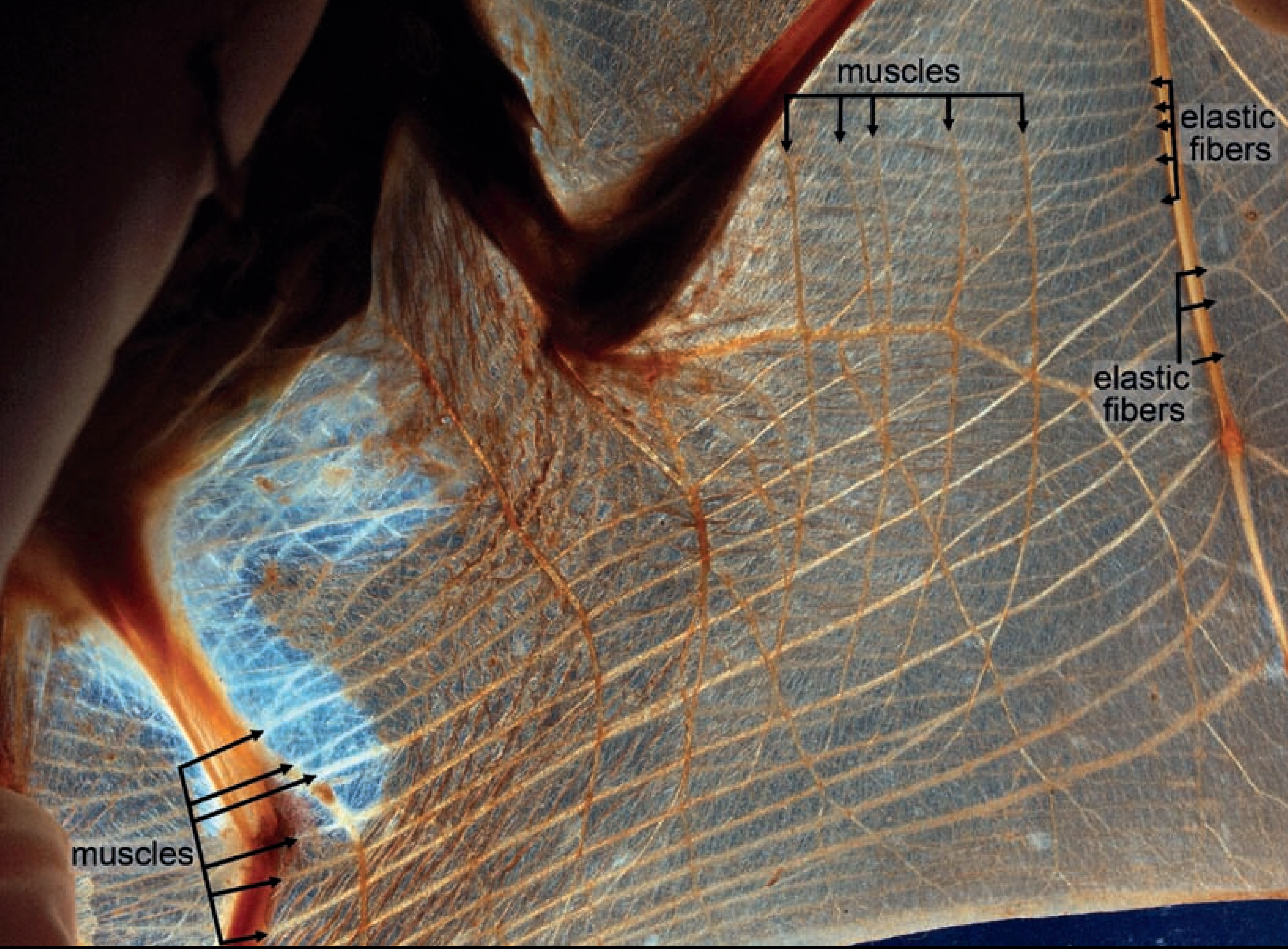
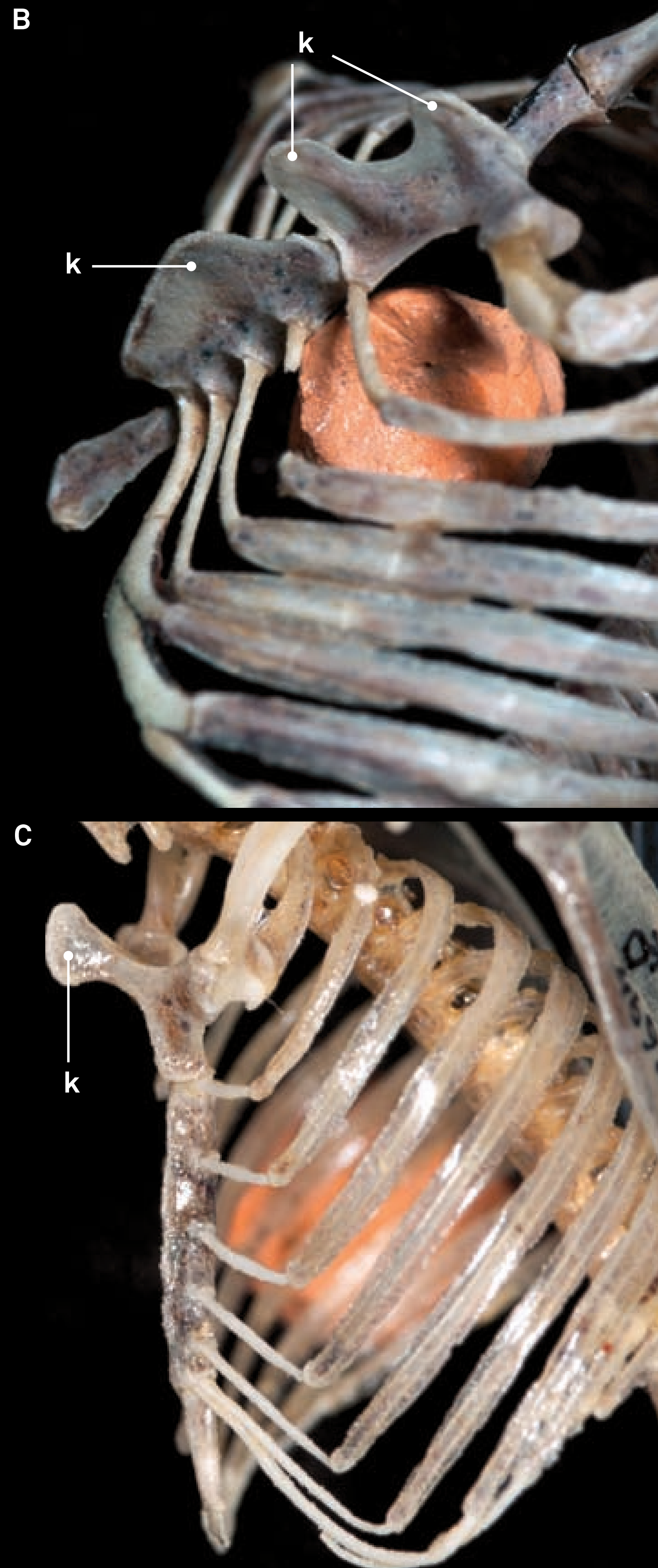


Figure 1.6.
Taken under polarized light, this photograph of the armwing of a Lesser False Vampire Bat (*Megaderma spasma*) shows both elastin and muscle in the bundles running perpendicular to the bat's bones. Photograph by Jorn Cheney, courtesy Sharon Swartz.

Figure 1.7.
A comparison of the breastbones and rib cages of a bird (**A**) Whip-poor-will (*Antrostomus vociferous*) and two bats, (**B**) Large Slit-faced Bat and (**C**) Sucker-footed Bat. Note the prominent keel (**k**) on the bird's breastbone (in **A**) compared to the arrangement of much smaller keels on the breastbones of the bats (**k** in **B** and in **C**). In the Sucker-footed Bat there is a single keel at the very top of the breastbone (**C**), while there are two keels (**k**) in the Large Slit-faced Bat (**B**) including an anterior one with two projections (two arrows) and a posterior one with a single projection. In **A**, the **u** is an uncinate process, features missing from the bats. (See page 20.)


B
k
k
k
C
k

Why should living birds lack teeth and lay eggs? Egg-laying in birds is not a specialization for flight, ~~it~~ is a form of reproduction inherited from ancestral reptiles. Pterosaurs also laid eggs. Egg-laying is a primitive trait also seen in a few mammals (the platypus lays eggs). Most mammals give birth to live young, and this form of reproduction evolved early in the mammalian radiation. Paleontologists have identified fossils from the Early Cretaceous (125–130 million years ago) as members of the large evolutionary group of mammals that today bear live young. Within this group, the placenta, another specialization, evolved by roughly the end of the Cretaceous (~66 million years ago). The placenta allows animals to retain a fetus inside the womb until it has grown quite large. Bats inherited a placenta and live birth from such non-flying mammal ancestors. For flying animals, carrying either a large egg internally (prior to laying it) or a fetus can impose energy costs due to the additional body weight that must be supported during flight. Although it only affects females, clearly females must survive for a species to continue! Weight constraints imposed by reproduction are something that all lineages of flying animals have had to overcome to be successful.

Teeth are clearly useful for obtaining, handling and chewing food and very important in most vertebrate groups. (See Chapter 5.) Teeth, however, are made of dense materials (enamel and dentine) and are amongst the heaviest structures in the bodies of small vertebrates. Because weight matters during flight, at least some lineages of flying animals—including all modern birds and some groups of pterosaurs—lost their teeth (in an evolutionary sense) after achieving flight. Instead, birds and most pterosaurs have (or had) keratinous beaks, which are lighter. Bats, however, retained a typical mammalian dentition that has been modified in different groups to facilitate processing of different foods. (See Chapter 5.) Teeth are smaller and sometimes fewer in bats that do not need to chew their food, *e.g.*, vampire bats and nectar-feeding bats. This may be due at least in part to the energy savings accrued by reducing the body weight of the animal.

The hind legs of bats also differ from those of birds and pterosaurs. Birds and pterosaurs are bipedal animals with long bones of their hind legs robust enough to bear the weight of a walking or running animal. In contrast, the long bones of the hind legs of most bats are slender and delicate, suitable for supporting a hanging animal but not for bipedal locomotion. Furthermore, the hip and limb structure of bats has been modified so that the hind legs are rotated relative to the pelvis such that the sole of the foot to face forward rather than backwards and downward as in most other animals. In birds, pterosaurs and other mammals the sole of the foot faces down. This difference is clearly reflected in the direction of flexion of knee joints and the position of a bat's feet. (Figure 1.8)

Figure 1.8.
This photograph of a flying Little Brown Myotis shows the position of the knee (arrow) as well as the hind foot. The hind limbs of bats are rotated so that the sole of the foot faces forward—in most other mammals, including humans, the sole of the foot faces backwards.

In birds that fly, two pairs of muscles largely power flight—a set of "elevator" muscles that raise the wings and a set of "depressor" muscles that bring them down. Both pairs of muscles are located on the surface of the chest (these comprise the white meat on a chicken). In contrast, in bats there are nine pairs of muscles involved in powering flight. The elevator muscles are located on the back, and the depressor muscles are on the chest. This difference probably explains why, compared to birds, bats are much thinner in profile through the chest—the flight musculature of bats requires broad areas for attachment to the rib cage, both back and front. The thin profile of the chest may have an added benefit in that it allows bats to squeeze into crevices and through small openings, giving them access to roosts inaccessible to many predators. (See Chapter 6.)

There are flightless species of birds and insects, but no known species of bats or pterosaurs is/were flightless. Flightlessness in birds and insects has often evolved on remote islands where there are few predators; the benefits of flight (in terms of providing access to resources and allowing long-distance movements) are reduced and there are additional dangers to flight, *e.g.*, individuals that fly high may be trapped by wind currents and blown away. But even bats living on remote oceanic islands in the South Pacific have retained their ability to fly. Nobody knows why this is the case. Although the structure of the forelimbs makes it difficult for most bats to walk effectively, strong walking and running behavior has evolved in some bats, *e.g.*, Common Vampire Bats (*Desmodus rotundus*). (Figure 1.9)

Brock Answers a Question

I'm often asked: "What is your favorite bat?" The problem with answering this is that, like many other bat biologists, I tend to be fickle. Today's favorite is tomorrow's also-ran. Working in the Yucatan Peninsula of Mexico in 1991, I was keen to meet some of the very neat bats that occur there. High on my list were Large-eared Woolly Bats (*Chrotopterus auritus*), Wrinkle-faced Bats (*Centurio senex*) and Tomes's Sword-nosed Bat (*Lonchorhina aurita*). On the third night, I was beside myself when a Wrinkle-faced Bat flew into the mist net. While I was busy with that bat, a Large-eared Woolly Bat flew into the net almost beside me. Within five minutes I also caught a Tomes's Sword-nosed Bat and my colleagues were kidding me about changing the battery in my pacemaker. By 9:00 pm that night, my three favorite bats were all in hand. By midnight, three other species I had not seen before were caught in the nets. So that night I had six favorite species.

Figure 1.9.
Two views of a Common Vampire Bat (**A** and **B**) on a treadmill illustrate the difference between the bat's running gait (**A**) and stance (**B**). When running, the bat reaches forward with its wrists and thumbs, swings its hind legs forward, plants them and repeats the process. Note that in **B** the bat is panting.

Figure 1.10.
A sample of faces and noses of bats. Included are (**A**) a Lesser Mouse-tailed Bat, (**B**) a Yellow-winged Bat (*Lavia frons*), (**C**) a Geoffroy's Horseshoe Bat (*Rhinolophus cliveosus*), (**D**) a Trident Leaf-nosed Bat (*Asellia tridens*), (**E**) a Bumblebee Bat (*Craseonycteris thonglongyai*) and (**F**) a Lesser Long-eared Bat (*Nyctophilus geoffroyi*), representing Mouse-tailed Bats (Rhinopomatidae), False Vampire Bats (Megadermatidae), Horseshoe Bats (Rhinolophidae), Old World Leaf-nosed Bats (Hipposideridae), Bumblebee Bats (Craseonycteridae) and Vesper Bats (Vespertilionidae), respectively. Photographs by Brock Fenton, Robert Barclay (**B**) and Sebastien Puechmaille (**E**).

Figure 1.11.
A sampling of noseleaves and ears in New World Leaf-nosed Bats (Phyllostomidae), including (**A**) a Jamaican Fruit Bat, (**B**) a Davis' Round-eared Bat (*Tonatia evotis*), (**C**) a Cuban Flower Bat (*Phyllonycteris poeyi*), (**D**) a Wrinkle-faced Bat and (**E**) a Common Vampire Bat.

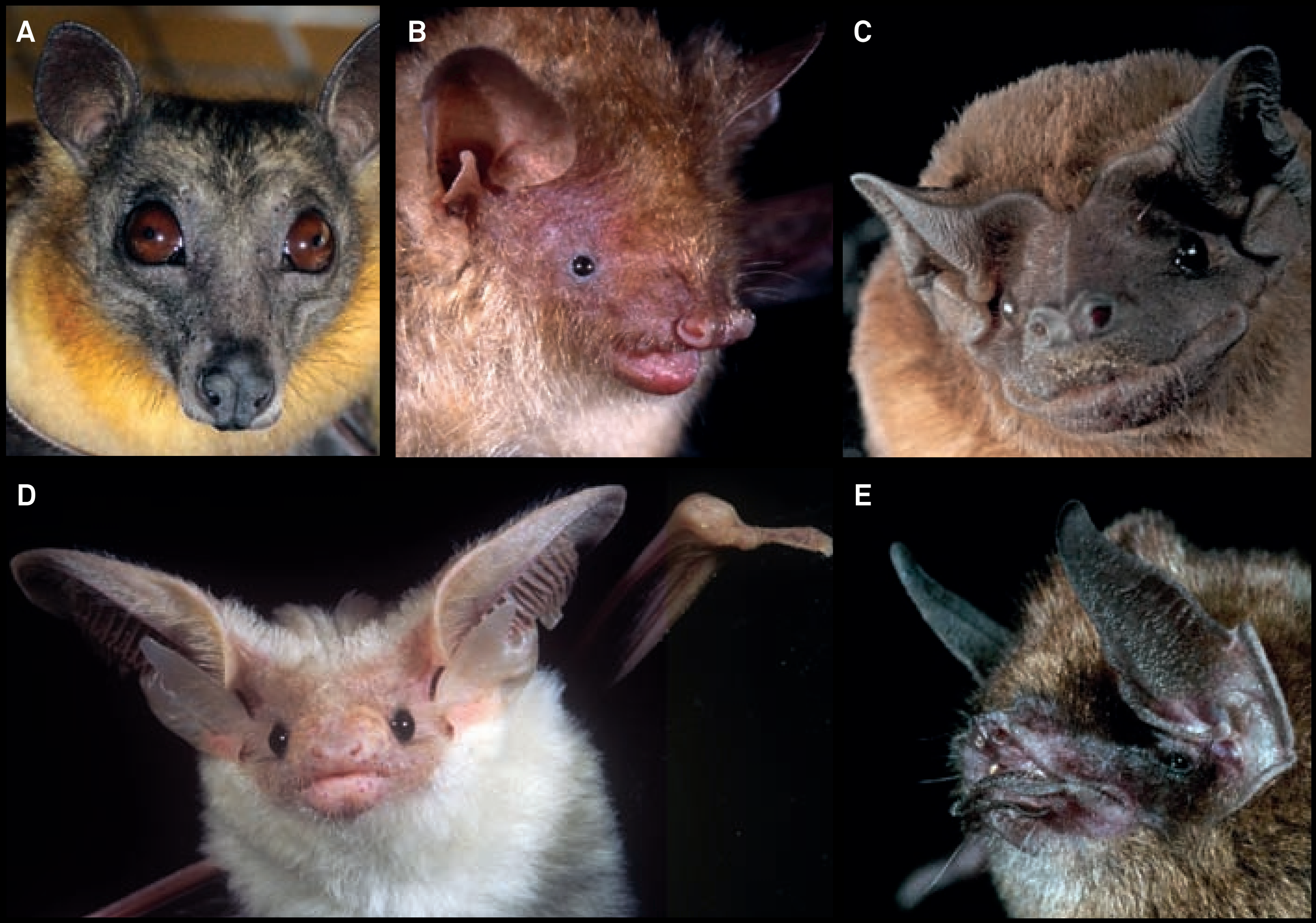


Figure 1.12.
Variations in the faces of bats, including (**A**) a Straw-colored Fruit Bat (*Eidolon helvum*), (**B**) a Greater Tube-nosed Bat (*Murina leucogaster*), (**C**) a Pallas' Mastif Bat (*Molossus molossus*), (**D**) a Hemprich's Big-eared Bat (*Otonycteris hemprichii*) and (**E**) a Sooty Moustached Bat (*Pteronotus quadridens*). Note variations in ears (**A**–**E**) and tragi (**C**, **D** and **E**).