Bats constitute one of the largest and most widely distributed groups of mammals, with a total of some 950 living species. In these respects they are second only to the ubiquitous rodents, and apart from the cold regions north of the Arctic Circle, the Antarctic, and a few isolated islands, there is no part of the world where bats are not to be found. They are unique among mammals in their mastery of true flight–a fundamental evolutionary step that opened the way to an entirely new and largely unoccupied part of the environment at least 55 million years ago. The opportunities presented by this vacant niche–nocturnal life, flight, insects and tropical fruits and flowers–allowed the bats to undergo a marked degree of adaptive radiation, evolving into an astonishing diversity in a relatively short period of time.

Initially, the early zoologists were concerned chiefly with recognizing and describing this multitude of species as they were discovered by advancing exploration, a process reaching a peak in the latter half of the nineteenth century and in the early part of the present century. In the past fifty years, however, scientists have turned their attention increasingly to the biology and physiology of bats. Although much remains to be studied, it is probably true to say that the basic biology of bats is at least as well known and in some ways better understood than that of most other groups of mammals.

Our objective in this book has been to present the general reader or serious student with a review of the fundamental aspects of bat biology. We have tried to demonstrate how bats conform to the biological principles common to all mammals, or have adapted and modified these to suit their own requirements. To accomplish this we have included relevant anatomical and physiological information set in an environmental and behavioural background, with some indication of the taxonomic and systematic foundation of the classification of bats as a whole. The study of bats and their natural history has been and to some extent remains esoteric, and a large part of this basic information is scattered through a wide diversity of original sources to which the general reader has no ready access. Throughout this book we have attempted to draw together the many threads that this vast mass of research contains, and to provide within a reasonable compass a comprehensive account of the natural history of these unique animals.

THE NAMES OF BATS

Vernacular names

Most peoples, even the most primitive, have names in their own languages for the many different plants and animals in their environment. In New Guinea, for example, local tribes often discriminate accurately between many different kinds of birds and mammals. Moreover, the majority of well known animals such as fish, lizard, frog, bird, rat or bat also have names in all of the major European languages. Usually these are modified by a descriptive word or words to define the animal concerned more accurately. Flying fish or Goldfish, Frilled lizard, Horned frog, Hummingbird, Black rat or fruit bat define more fully the animals to which they refer. Sometimes such multiple names may provide even more information, as for example Long-tailed Giant rat, or Spotted-winged fruit bat. These are known as vernacular or common names.

Although many animals, including bats, have English vernacular names, many others do not. Also, a vernacular name can be applied to more than one kind of animal and this can easily lead to confusion, while such names do not necessarily have the same meaning in different languages. In this book English vernacular names have been used whenever possible, but are followed (in parentheses) by the appropriate scientific name to avoid these difficulties. Where no commonly accepted vernacular name is available we have used the scientific name, and in a few cases for clarity and brevity scientific names have been employed rather than the vernacular.

Scientific names

The scientific names of plants and animals are always written in Latin, partly because this was the common language of early naturalists who began the process of formal description, and also because although now archaic, Latin is internationally accepted for this purpose to overcome the problems of translation.

Scientific names (usually printed in italic typescript) have two important elements, the first or generic name that indicates the relationship of the species concerned to other species, and a second or specific name that signifies the particular species in question. Sometimes a third or subspecific name may be used to indicate small variants within the species, as for example slightly differing populations of the same species on different islands. Latinized scientific names are frequently but not necessarily derived from roots in classical Greek and often suggest the nature of the organism to which they refer, or draw attention to some significant feature or habit. Sometimes a name indicates the geographical region whence the organism came, or may commemorate a person, possibly the naturalist who discovered it. Scientific names do not have to be constructed in this way, however, and can be quite arbitrary.

Among bats, scientific names often involve *Nycteris*, the Greek word for bat, perhaps an obvious choice. Not only is it used unornamented as the generic name for the Slit-faced or Hollow-faced bats of Africa but it has also been used as a root for numerous other generic names such as *Nanonycteris* or 'Dwarf bat', *Eonycteris* or 'Dawn bat' and *Hylonycteris*, a 'Wood bat' or 'Forest bat'. The allusion in a name may be oblique as in *Chironax*, from the Greek word meaning 'one who is master of his hands', a reference to bat flight. Scientific names can be very descriptive, *Saccopteryx bilineata* for instance referring to the wing sacs and to the two stripes on the back of the bat to which it applies. *Laephotis wintoni* is the Large-eared (literally 'sail-ear') bat named after the naturalist W. E. de Winton, *Laephotis angolensis* its relative described from Angola. Bats boast the shortest scientific name among mammals - *Ia io*, proposed by the mammalogist Oldfield Thomas reputedly for its brevity, in response to a challenge to produce the shortest possible name. *Io* was a young woman of classical times and Thomas apparently considered many women of that age to be essentially flighty, like bats.

Species, genera, families, suborders and orders

The species is the lowest major category in classification and the many different species of bats are recognized by such features as differences in body or skull size, in colour, in such structures as their noseleaves or ears, or by small differences in cranial or dental morphology. Such features are used by the taxonomist to determine to which species any given bat belongs and to indicate relationships to other species. Often the differences between species are very small and quite subtle, and careful study is required to distinguish them, particularly when closely related species occur together. Occasionally a clue is provided by some apparently quite unrelated circumstance, as for example by the small mites that infest the dental membranes of *Leptonycteris nivalis*, a species of American Long-nosed bat. These cause small pits to appear in the bony palate near the teeth, the like of which are not found even in the closely related species *Leptonycteris sanborni*.

Genera as a rule bring together species with common similarities but occasionally have only a single, prominently characterized species. They are customarily recognized by more far reaching external, cranial and dental characters, different workers placing a greater or lesser emphasis on different features. The wide range of variation found in bats has led to a large number of recognized genera, although sometimes these are based on relatively small differences. The family usually unites a number of related genera but again some bat families contain only one especially distinctive and isolated genus. Genera are sometimes divided into two or more subgenera, and families similarly into subfamilies. Family names always have the termination *idae* i.e. Phyllostomidae, while subfamily names have the suffix *inae* as their ending i.e. Glossophaginae. At this level, skeletal structure, with special emphasis on the skull and on the bony structures associated with the shoulder and wing, provides much of the basis of classification. Currently some 950 species of Recent bats are recognized, grouped into perhaps 190 genera, but these numbers vary slightly from one authority to another since the limits of the species and especially of the genus are subjective. Depending on the emphasis given to the features adopted for further classification, the modern genera are grouped variously in 17, 18 or 19 families, which themselves constitute the two major groups or suborders of bats, one the Megachiroptera or Old World fruit bats, including but one family, and the other the Microchiroptera, basically insect-eating bats, including all of the remaining families. Together, the two suborders form the order Chiroptera, itself a major division of the class Mammalia.

A resurgence of interest in the study of bats and in their relationships with each other at all levels of classification has led to the application of new and modern techniques, such as the study of bat chromosome patterns, comparison of the composition of the blood in different groups of bats, or detailed studies of bat parasites. This research is suggesting ways in which the traditional classification might be changed, especially at the familial and generic

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levels. A particularly good example concerns the true vampire bats of the New World, so much modified for an exclusive diet of blood obtained by biting other animals that they have long been considered to represent a family of their own, the Desmodontidae. Studies of their chromosomes, the properties of their blood, the morphology of their sperm, their echolocation system and parasites have indicated a close affinity with certain members of another New World family, the Phyllostomidae. As a result, most authorities now consider that the vampire bats should be more correctly classified as a subfamily of the Phyllostomidae, rather than as an independent family. The traditional classification is also being challenged by new ways of assessing taxonomic characters and indeed by widening their range to include a greater variety of the morphological features of the hard and soft anatomy. The relatively recent recognition of familial status as the Mormoopidae for the Naked-backed, Moustached and Ghost-faced bats of the New World is an example of this kind of study and similar research is widening our understanding of the relationships and classification of the nectar-feeding bats of the New World family Phyllostomidae. Such studies often employ computer techniques and the increasing use of these and of computer-based statistical analysis is broadening and extending our knowledge of geographical variation within the species and of interspecific differences in bats, as well as helping to illuminate and unravel their relationships at higher levels of classification.

Sources

In attempting this factual survey of many facets of the biology of bats we have relied upon many sources ranging from the abundant literature on this subject to discussions with colleagues and personal experience. Published information about many aspects of the biology of these fascinating animals has increased annually very rapidly over the past two or three decades and it is probably correct to say that more papers and books about bats have appeared in the past 25 years than in the century preceding this period. This increase is basically the result of a greater awareness of bats as research subjects, of the development of more effective techniques and equipment for studying them and of improved opportunities for field and laboratory work, together with a wider recognition of the need to understand and conserve the unique natural resource that bats represent. We have been fortunate, however, that as a principal reference for a number of chapters of this book we have been able to rely upon the excellent volumes *Biology of bats* edited by W. A. Wimsatt and published in 1970 and 1977 by Academic Press, New York. The numerous articles by specialist authors that these books bring together provide not only an unrivalled source of biological information but also a detailed and comprehensive bibliography of each topic.

Clearly, to detail every published study that we have consulted in the preparation of a book of this nature would greatly complicate and lengthen the text. Instead, we have provided, in a terminal bibliography, a list of the major works that are concerned with bats in the broadest sense. Faunal studies giving general accounts of bats of various parts of the world are also included. To these we have added a chapter by chapter bibliography that details the major reference or references that we have used, together with any later studies that have been relevant or seemed pertinent. We have tried to ensure that as major sources we have included one or more papers with an extensive bibliography that will provide the reader with a further overview of the topic concerned.

Chapter 2 Form and structure

Bats are mammals and, as such, possess all of the features characteristic of this vertebrate class. These features include most notably: possession of a body covering of hair (pelage or fur) as opposed to scales (reptiles) or feathers (birds); mammary glands for the production of milk which is used to suckle and nourish the newborn young prior to the development of its own ability to acquire food; a single bone (dentary or mandible) constituting the lower jaw as opposed to the complex of bones found in the lower jaws of other terrestrial vertebrates such as reptiles and birds; three ear bones or ossicles (named for their shape, malleus–hammer; incus–anvil; stapes–stirrup)

in the middle ear region; the single replacement of at least a portion of the dentition (milk teeth); and the ability to maintain a constant body temperature (warm-blooded). In addition, bats belong to the large and progressive infraclass Eutheria (placental mammals that give birth to young after a substantial period *in utero* where they are maintained and nourished by means of a specialized embryo-maternal structure called the placenta). This general scheme of reproduction is in marked contrast to the relatively more primitive modes of egg-laying found in the monotremes (Duck-billed platypus and Spiny anteater) or that found among marsupials (Kangaroos
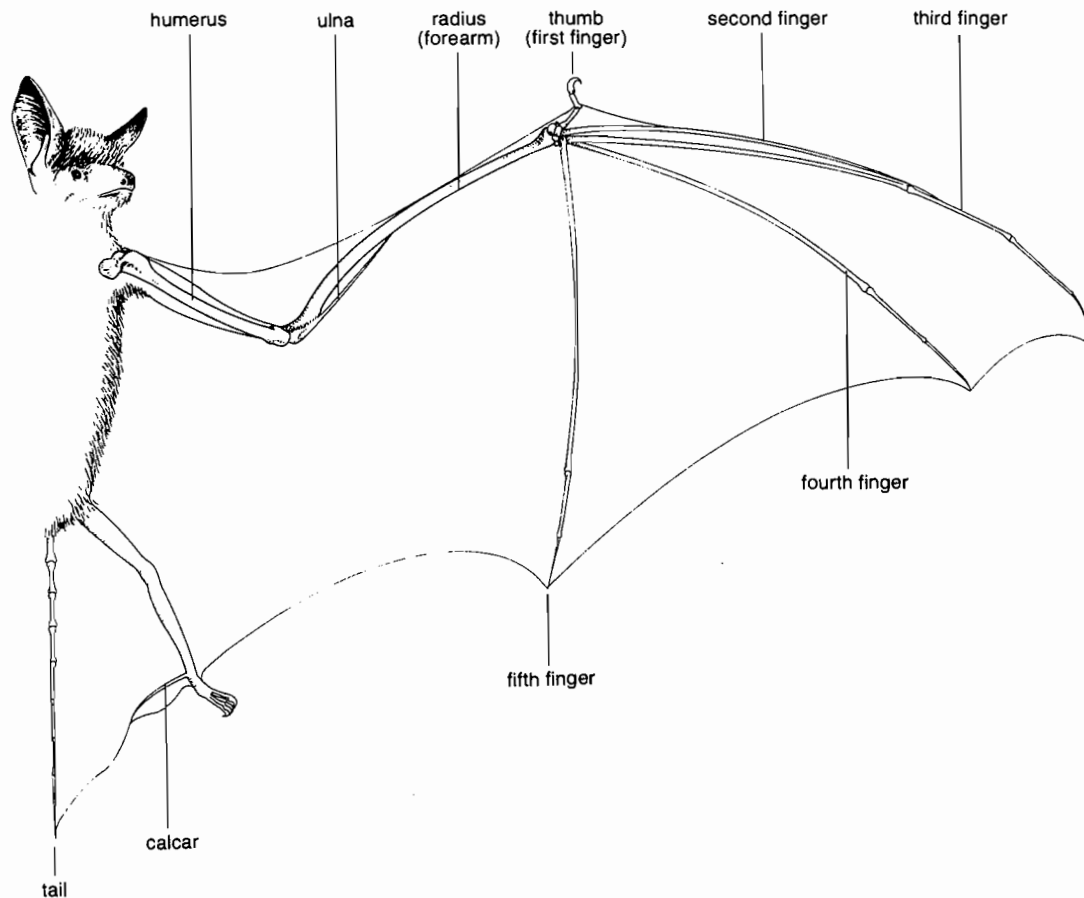

Fig. 2.1 *Structure of bat wing.*

and Opossums) in which the developing young passes a brief gestation period *in utero*, is born, and then spends a substantial period of its postnatal life attached to a teat in its mother's specialized pouch.

Since bats are mammals, it is true that their form (anatomy, both external and internal) is basically like that of other mammals. However, their adaptation to true flight (especially in darkness) has resulted in their unique form and appearance. They are easily recognized as the only winged or flying mammals. In this chapter we shall examine the unique form of bats. In subsequent chapters we shall explore in more detail some of their particular adaptations including such things as flight, echolocation, feeding, and thermoregulation (hibernation).

EXTERNAL FORM

The wing and associated flight membranes

The wing of a bat is perhaps the singlemost diagnostic feature of this unique group of mammals. It supersedes nearly all of their other less obvious, but perhaps more interesting, special adaptations. We shall discuss the functional aspects of bat wings in Chapter 4; here we describe the general structure of the wing and other associated flight membranes.

Unlike birds and the extinct flying reptiles (Pterosaurs) in which the bony (skeletal) structure of the wing comprises greatly modified forelimb bones, the wing skeleton of bats is not much different from that of the forelimb of most normal mammals (Fig. 2.1). By comparison, a bat's wing is not as drastically modified (skeletally, at least) as the forelimb of a horse, deer, elephant, or whale. As the Greek name for the order Chiroptera (hand wing) implies, the wing is simply a modified hand. The skeletal elements, and indeed much of the soft anatomy in the wing of a bat, may be directly compared to the arm and hand of a human.

The upper arm bone (humerus) is essentially the same as that found in all mammals. This bone articulates at the shoulder joint with the shoulder blade (scapula). The muscles that bind and move this bone are essentially the same, although proportionately larger, than those found in man. Of all the wing bones, the humerus is less elongated, relatively, than any of the others.

The forearm of bats illustrates the first in a series of specialized modifications. In typical mammals and other four-footed terrestrial vertebrates the forearm comprises two bones, the radius and ulna (Fig. 2.1). These two bones articulate with the humerus in the elbow region and, in humans, are constructed in such

a way as to allow the turning of the hand from a palm down position (pronation) to a palm up position (supination). In bats, the ulna is greatly reduced in size and it appears as a thin thread-like bone fused to the much larger and elongated radius. The articulation of the forearm and humerus at the elbow is dominated by the greatly expanded radius (Fig. 2.2). The olecranon portion of the ulna is the largest vestige of this bone and is usually fused to the radius. Its primary function is to lock or otherwise stiffen the elbow joint when the wing is extended and being used in the power generating portion of the wing beat. Overall, the forearm of bats is greatly elongated compared to other mammals. In some bats, especially those with very long wings, the length of the forearm may be nearly equal to the combined length of the head and body. Because of the structural requirements of rigidity and strength to withstand the enormous air pressures developed during flight, the radius has lost its ability to rotate (pronate and supinate).

The wrist region of bats is essentially the same as in other mammals. However, it is less flexible because the ulna is reduced and the radius has lost its rotational ability. The many carpal bones in the wrist are shaped and articulate in such a fashion as to allow restricted movement in the forward and backward
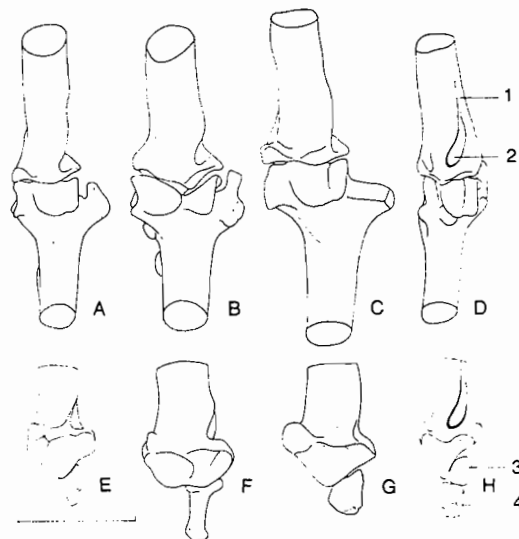

Fig. 2.2 Anterior view of elbow regions of four bats. A, Pteronotus parnellii *(Mormoopidae); B,* Mormoops megaphylla *(Mormoopidae); C,* Artibeus toltecus *(Phyllostomidae); D,* Molossus molossus *(Molossidae). Below each (E–H) the articular facets of the radius are shown. 1, radius; 2, flexor fossa for the attachment of the biceps brachii and brachialis muscles; 3, reduced ulna; 4, sesamoid (extra) bone. Line below E is 4 mm in length.*

plane (extension and flexion, respectively). This is another apparent adaptation to withstand the tremendous buckling forces that are placed on all wing joints during flight.

Except for the great elongation of the bony elements (phalanges), the hand portion of a bat's wing is not markedly different from the structure of the human hand (Fig. 2.3). The thumb is perhaps the least modified of all of the digits. It is directed more forward than in the human hand and bears a strong terminal claw in nearly all bats: in one family (Furipteridae) the claw is minute and apparently functionless and in another (Myzopodidae) there is only a rudimentary claw. The length of the thumb varies considerably among bats, being very short in some microchiropteran families (Natalidae, Furipteridae, Myzopodidae and some Vespertilionidae) to relatively long in the Old World fruit bats or flying foxes (Megachiroptera). In the latter, the thumb is extremely mobile and is regularly used in locomotion, food handling, and fighting. Vampire bats (Phyllostomidae) crawl, hop or jump quite readily. Like Old World fruit bats they also have relatively long and strong thumbs which are used to help lift the bat and pull it forward when crawling and which play an

important part in helping to provide thrust when these bats hop or jump. The second digit or index finger in bats is composed primarily of a long metacarpal element (main bone of the human palm). One or two short phalanges (finger bones) may be found in this digit. In most Old World fruit bats (Megachiroptera), this digit terminates with a strong claw but in some the claw is reduced in size or absent. The terminal claw on the second finger is absent in all microchiropterans except the fossil species *Icaronycteris index* and, perhaps, *Archaeonycteris trigonodon*. The third, fourth, and fifth fingers are essentially the same in overall structure, the largest element in each being the elongated metacarpal. The number of phalanges in the third finger varies from two to three and there are only two bony phalanges in the fourth and fifth fingers. None of these three fingers has a claw. The length of the finger bones varies from one family to another and this variation produces wings of different shapes and apparent flight potentials.

The flight surface of the wing of bats consists of a flexible membrane stretched around and between the skeletal framework just outlined (Fig. 2.3). This membrane is anchored at the point of the shoulder and extends along the upper arm and forearm to an
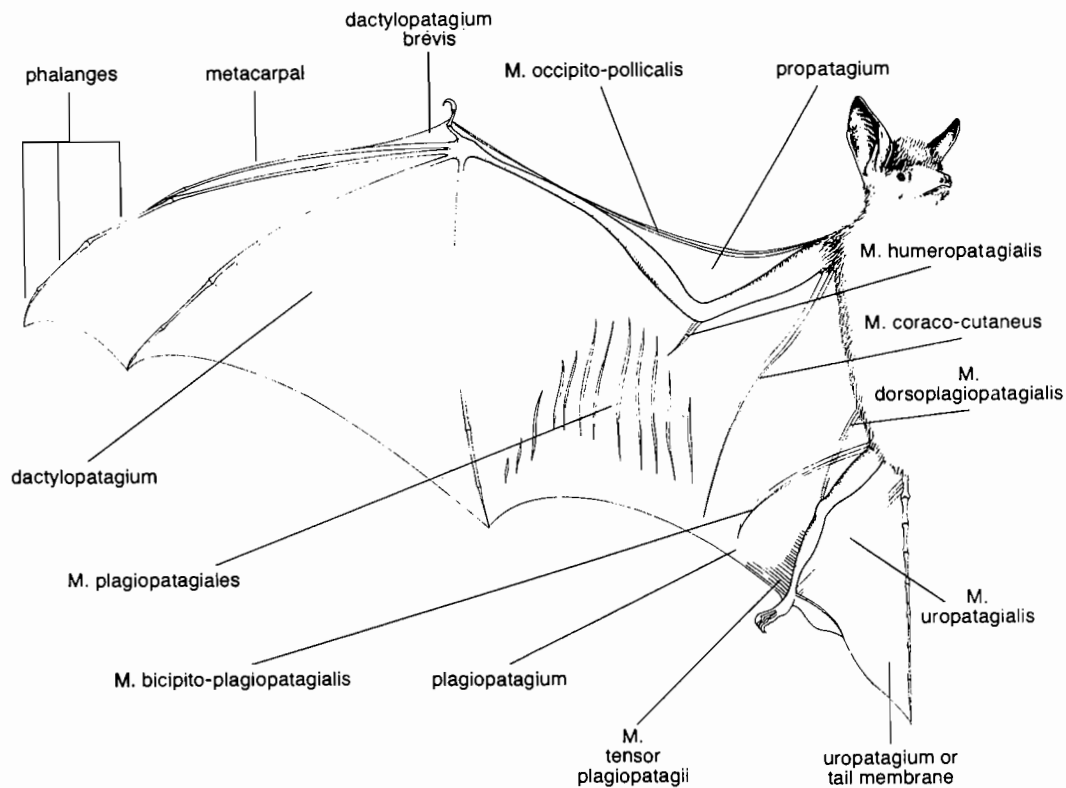

Fig. 2.3 *Flight membranes and the major muscles that help to keep them taut. Some of the muscles shown do not occur in all bats.*

attachment at the base of the thumb. The leading edge of this portion of the wing membrane incorporates a special muscle (M. occipito-pollicalis) which, when it contracts, causes a general down-turning and increase in the surface area of this portion of the wing. This flight surface–the propatagium–is used to increase or decrease the aerodynamic curvature (camber) of the wing. The portion of the wing membrane forming an elastic webbing between the fingers of the hand is called the dactylopatagium or chiropatagium and a small segment of this membrane extending from the thumb to the second finger is sometimes called the dactylopatagium brevis. It and the propatagium form the leading edge of the wing. The flight membrane that extends from the sides of the body, hindlimb, and foot, along the rear portion of the upper arm, forearm, and fifth finger is called the plagiopatagium. The camber or curvature of the dactylopatagium and plagiopatagium is controlled by the degree of flexion of the fingers and body axis.

As a general rule, the wing membrane attaches to the body along the side. Occasionally, the attachment of the wing membrane may be located rather high on the flank or, in several species, the wing membranes unite and attach on or near the centre of the back to give the back a naked appearance. This condition is found in several megachiropterans (*Pteralopex*, *Dobsonia* and one species of *Rousettus*) and in several microchiropterans of the genera *Pteronotus* and *Cheiromeles*. The function of this peculiar wing attachment is not known, but it may allow an increase in effective flight surface without adding to the total span of the wing.

The effective area of the wing membrane may be augmented by an associated flight membrane that is not directly involved in the structure of the wing proper. This consists of a membrane–the uropatagium or interfemoral membrane–stretched between the hindlimbs and tail (Fig. 2.3). In many bat species, the uropatagium may be further supported by a long cartilaginous spur (calcar) that articulates with the heel of the foot (Fig. 2.1) and which may enable an increase in its area. The form and extent of the uropatagium and the presence or absence of a calcar varies among bat species (Fig. 2.10).

The membranes of the wing and uropatagium are simply extensions of the general body integument (skin) and, as such, have an outer epidermis (cornified layer) and an inner dermis (vascular layer). The flight membranes are especially thin (Table 2.1) and translucent to light in most cases. The dermal layer has a higher than usual concentration of elastic fibres and intrinsic, striated (voluntary) muscle bundles. These anatomical features provide the necessary elasticity and flexibility of the flight membranes which must be held taut during flight and be easily collapsible when the wing is not in use.

Although the flight membranes are delicate in appearance, they are comparatively tough and resilient as they must be able to resist tearing and puncture by sharp objects such as thorns and twigs often encountered in the bat's feeding or roosting environs. Table 2.1 shows the tensile strength of the flight membranes of several bat species compared to those of rubber surgical gloves and commercial plastic sandwich bags. Whereas the rubber gloves are thicker and considerably more elastic than wing membranes, they are more prone to puncture than are

TABLE 2.1 Some physical properties of bat wings compared to other materials.

Subject	N	Thickness (mm)	Puncture strength (kg/mm)	Elasticity (mm/kg)
Rubber glove	10	0.234	2.80	35.1
Sandwich bag	10	0.020	8.63	18.7
Myotis lucifugus	10	0.030	5.81	14.0
Myotis thysanodes	10	0.243	9.37	12.9
Myotis yumanensis	3	0.023	7.28	15.5
Eptesicus fuscus (adult)	7	0.038	9.72	9.5
Eptesicus fuscus (young)	8	0.034	5.62	14.0
Plecotus townsendii	1	0.032	7.19	12.3
Antrozous pallidus	2	0.033	7.72	11.9
Tadarida brasiliensis	1	0.063	3.00	15.4

Numbers are mean values; *N* - number examined. Puncture strength determined as the weight (kg) required to puncture membrane per mm of membrane thickness. Elasticity determined as mm of depression per kg of weight added. (After Studier, 1972).

bat wings. On the other hand, plastic sandwich bags are about equal to wing membranes in thickness, only slightly more elastic, and have nearly the same puncture strength. This table also illustrates the relative high elasticity and low puncture strength of the flight membranes of young Big Brown bats (*Eptesicus fuscus*); adults of this vespertilionid species have tougher, less elastic membranes. The wing membranes are generally stronger and less elastic in bats that feed on the ground or in and around thorny vegetation such as the Pallid bat (*Antrozous pallidus*), Fringed myotis (*Myotis thysanodes*), or Big Brown bat.

One might wonder about the extent and frequency of damage to bat wing membranes. Although there is little quantitative information on the matter, a number of bat biologists have noted a rather high incidence of healed scars from tears or punctures in the wings of captured bats. Some individuals have been captured with as much as 10-20 per cent of the wing-tip missing. Wound healing in these delicate membranes is apparently quite rapid.

The flight membranes are generally naked in appearance, although microscopic examination reveals many short, transparent hairs on both the upper and lower surfaces. Specialized bands of bristles may be found on the underside of the uropatagium of some species and these are thought to form an 'insect trap' used during in-flight foraging. Other specialized bands and fringes may be found on the upper surfaces of the wing. These may facilitate the airflow over the wing during flight. The body fur may extend onto the upper surface of the wing along the upper arm and forearm, or out onto the plagiopatagium adjacent to the attachment of the wing on the sides of the body. In a similar manner, the uropatagium may be partially furred. In the North American tree-dwelling bats of the genus *Lasiurus* and the Asian Tube-nosed bats (*Murina*), the proximal portion of the plagiopatagium and the uropatagium is densely clothed with hair.

The wing and associated flight membranes are usually black or greyish brown in colour, but in some African vespertilionids such as the Light-winged Lesser House bat (*Scotoecus albofuscus*) and White-winged bats (*Eptesicus tenuipinnis* and *E. rendalli*), the wing membranes are white or greyish white. Whitish wings also occur in the African molossid *Tadarida pumila* and the Neotropical emballonurid *Diclidurus virgo*. White wing-tips are commonly found among members of the New World leaf-nosed bats (Phyllostomidae). Yellow and white spots are found on the wings of the Tube-nosed fruit bats *Nyctimene* and *Paranyctimene* which live in the Indo-Australian region. The wings of some species of the vespertilionid genus *Glauconycteris* are ornately variegated with cream white, light browns, and shades of black. In the African vespertilionid, *Myotis welwitschii*, and the Papuan Black-bellied fruit bat, *Melonycteris melanops*, the wings are rich reddish-orange. And, the wings of the Painted bat (*Kerivoula picta*) have highly contrasting orange and black markings (Fig. 2.4). The function of such beautifully coloured wings and ornate body colour patterns is not well understood. These animals are colour-blind and active at night. Presumably, these markings may serve a protective or camouflage function in those species that roost in trees or other exposed sites. Perhaps, in the case of white wings or wing-tips, the contrast may serve a disruptive function to confuse nocturnal and/or crepuscular avian predators such as owls and hawks.

While it is true that the primary purpose of the wing and associated membranes is flight, these specialized features also serve a number of non-flight functions. Several species of vespertilionids (*Myotis*) have been observed (with the use of high speed
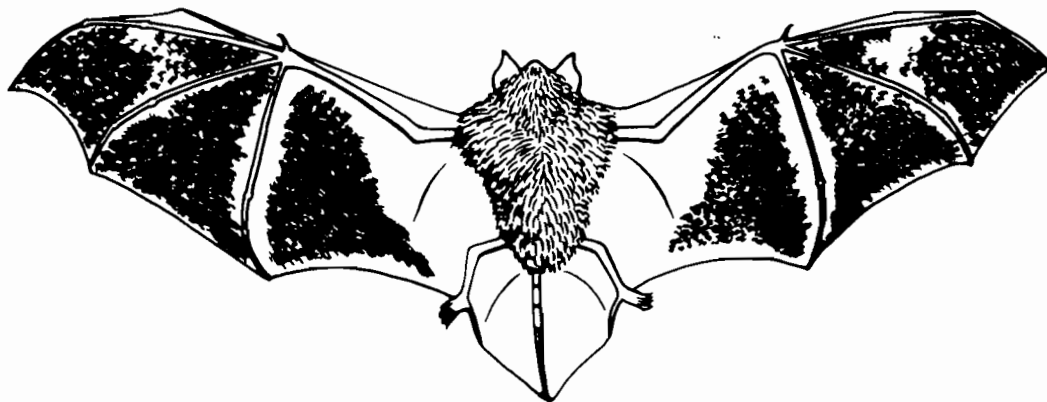

Fig. 2.4 Wing coloration of painted bat (Kerivoula picta – *Vespertilionidae*).

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motion pictures) using the wings to capture insects in flight. In these film sequences, the wing is used much like a tennis racket is used as an extension of the human arm, to deflect insect prey toward the mouth or into the basket-like pocket formed by the hind-limbs, tail and uropatagium. In the course of this 'fielding' behaviour, the bat may collapse both wings around the body, tuck the head into the uropatagium, and perform an aerobatic somersault.

The wings possess a rich supply of blood vessels that serve to transport oxygen and nutrients to the flight muscles. In addition, this expansive vascular network may also radiate excess heat and thereby function as a cooling device. Some flying foxes, such as *Pteropus*, roost in trees and are exposed to the high temperatures of the noonday sun. These bats have adopted a behavioural use of the cooling ability of their expansive wing surfaces. Under high heat stress they urinate on their wings which are tightly folded around their bodies and use the effect of evaporation to cool themselves. This blade, however, has two edges. Certainly, the dissipation of excess heat is to the bat's advantage. On the other hand, the un-controlled loss of heat would be a marked disadvan-tage, especially during flight on cool nights. The Western Pipistrelle (*Pipistrellus hesperus*) of the south-western regions of the United States regularly flies on winter nights in air temperatures as low as $-5°C$. Such heat loss problems will be discussed in Chapter 6.

Another function of the wings, also associated with the rich vascular network, is one of gas exchange. During flight a great deal of carbon dioxide is generated as a by-product of the high metabolic activity of the flight muscles. Normally, in mammals, this excess excretory product is exchanged in the lungs through normal respiration. Bats also do this. However, it has been shown that individual Big Brown bats (*Eptesicus fuscus*), at rest and at 18°C, exchange 0.4 per cent of their total carbon dioxide production through the wing membranes. Active individuals of this species, at 27.5°C, dissipate 11.5 per cent of their carbon dioxide production via these membranes. This is a direct result of the thinness of the membranes and their rich blood supply. One might wonder if oxygen might also be taken in across the wing membranes; that is, do the wings serve a true respiratory function? The answer is no. In order for oxygen to be efficiently exchanged, it must first be dissolved in water as in the case of a fish's gill or in the moist environment of the lungs. As wing mem-branes are dry, oxygen exchange is insignificant. Although the wings are the most immediately obvi-ous features of bats, they are by no means the only interesting characteristic of these unique mammals.

The head

Perhaps more than any other group of mammals, bats display a wide range of variation in the shape of the head. Consider for a moment the general lack of variation in head shape among wild or domestic hoofed mammals–horses, deer, and antelope. Also note the generally stereotypic shape of the heads of dogs and cats (non-domestic) and rabbits. Birds also possess a generally recognizable head shape. True, they do vary in the shape and size of such features as beaks and eyes. The lack of variation among some groups of mammals and the beak variation observed in birds all reflect adaptations to particular diets or food-getting behaviour. Hoofed mammals all utilize food items that require a fair amount of chewing, and so tend to have long muzzles that reflect their long jaws which support long and massive batteries of grinding teeth. Similarly, hummingbirds, hawks, and ducks exhibit a range of beak variation geared to specific food capture and utilization mechanisms. The wide range of variation in the shape of bat heads also reflects a wide variation in diet and food capture.

The ancestors of bats, or at least of microchiropte-rans, are thought to have been insectivorous (catch-ing and feeding on insects). Insectivory is wides-pread among bats and is perhaps the most common food habit (approximately 70 per cent of the living species of bats are insectivores). Generally speaking, bats with this kind of diet have moderately long, pointed noses. The eyes are small and the back part of the head is round in appearance. Variations on this general theme appear to correlate with the kinds of insects utilized in the diet. Those bats that eat soft-bodied insects such as moths, mosquitoes, and other small flies may have slightly longer, shallow muzzles or their faces may be short and broad. Bats that eat hard-bodied insects (such as beetles) may have somewhat shorter and deeper muzzles, and the back of the head may be wide and highly domed. The width and domed appearance of the back of the head is usually associated with moderate to high crests and ridges or a greatly expanded braincase surface. All of the modifications relate directly to increasing the size of the temporalis muscle used to operate the massive jaws in the chewing of these hard-bodied insects.

Some bats, approximately 0.7 per cent of the living species, are carnivorous (eat flesh) and this is reflec-ted in the shape of their heads. For example, the head of the American False Vampire (*Vampyrum spectrum*–Phyllostomidae) is dog-like in appearance. While less dog-like in overall appearance, other carnivorous bats such as *Macroderma gigas* (Megadermatidae) and *Phyllostomus hastatus* (Phyllostomidae) have long, stout muzzles and long, rounded heads. Fish-eating

or piscivorous bats (approximately 0.6 per cent of all living species) such as *Noctilio leporinus* tend to have short, deep faces and high-domed heads like bulldogs. Indeed, the common name for this particular species is the Bulldog bat. On the other hand, the head of the fish-eating vespertilionid *Pizonyx vivesi* is not markedly dissimilar from its insectivorous relatives.

Frugivory (fruit-eating), the second most common chiropteran diet (approximately 23 per cent of the living species), also results in a wide range of head shapes. Among the Old World fruit bats (Megachiroptera), the snout may be long, deep, and pointed, with the rear portion of the head widely rounded. This is the case in *Pteropus*, *Rousettus*, and *Dobsonia*. Among the New World leaf-nosed bats (Phyllostomidae), this general head shape is exemplified by *Phyllostomus discolor*, *Carollia perspicillata*, and *Brachyphylla cavernarum*. This head shape may be generally primitive and, like that of hoofed mammals, provide room for the massive grinding teeth (molars). On the other hand, another expression of frugivory in the shaping of the head is a trend toward the extreme shortening of the face and high doming of the braincase. A full spectrum of variation occurs between these extremes. In such bats as the phyllostomids *Centurio senex* and *Ametrida centurio*, the face is very broad, nearly flat (monkey-like), and the back of the head rises sharply above the level of the eyes (Fig. 2.8).

Among the most curious of head shapes in bats are those found in the nectar and pollen eaters (nectarivory, approximately 5 per cent of the living species). In these, the muzzle is long and tubular and the back of the head is low and rounded. As in hummingbirds (which are the avian and diurnal equivalent of these bats), there is a wide range of variation in snout length. The phyllostomid *Musonycteris harrisoni* is perhaps the most extreme in this regard, with a snout that is nearly two and a half times the length of the braincase.

Whereas the shape of the head generally reflects the dietary habits of bats, other considerations also may influence the shape of the head. One particular roosting habit, that of occupying tight spaces such as narrow rock crevices or the hollow internodes of bamboo, is associated with a trend to flattened heads. Extremes in flat-headedness are seen in the vespertilionid Bamboo bats (*Tylonycteris pachypus* and *T. robustula*), and the rock-dwelling molossid Flatheaded bats (*Sauromys petrophilus* and *Platymops setiger*). Aerodynamic considerations (especially among the swifter flying bat species) may influence the shape of the head. In these, the shape of the head is fusiform (bullet-shaped, or at least conical), while slow-flying bats display a wider range of head shapes that are presumably less restricted by aerodynamic forces.

Associated with the head are a number of other features that add to the wide range of appearances of bats. These include the ears, eyes, nostrils, and various facial excrescences which are collectively referred to as noseleaves.

The ears

In most mammals, and other vertebrates as well, hearing is an important sense for determining various aspects of the surrounding environment. In the lighted diurnal world, hearing acuity may be superseded by visual perception. For bats, the majority of which hunt or otherwise orient in their environment by means of acoustic perception (echolocation), hearing is of paramount importance. We will discuss acoustic orientation in Chapter 8. Here we will examine the variation in size and shape of the external ears (pinnae) and associated structures.

Ear shape among the megachiropterans is not especially variable nor very spectacular. The ears of these bats are usually short and generally rounded. Some species, such as those of the genera *Pteropus* and *Dobsonia* may have long, somewhat pointed ears. For the most part, the ears of these bats are not strikingly disproportionate in size compared to the head and body. At their base, where they join the head, the ears of megachiropterans form a complete ring; that is, they are tubular. The external pinnae of these bats are never connected and a wide array of voluntary integumental (skin) muscles allow a considerable range of independent movement of the ears. While hanging in the roost or being held in a captor's hand, the ears are constantly twitching and moving about. Megachiropterans are thought to orient primarily by vision and this may account for the lack of specially adapted ears. Even the ears of *Rousettus*, which is known to have a crude form of echolocation, are not noticeably different from those of other megachiropterans.

In contrast to the Megachiroptera, the Microchiroptera display a wide range of variation in ear shape and size. Some are quite bizarre. Before discussing these variations, it is necessary to describe the components of microchiropteran ears. The bulk of the ear is composed of the large flap-like external pinna (Fig. 2.5). Unlike the megachiropterans, the base of the pinna of microchiropteran ears is generally open at the front; that is, not forming a complete ring or tube. The inside surface of the ear conch frequently has several transverse ridges or a series of longitudinal ridges. The function of these is not known, but they
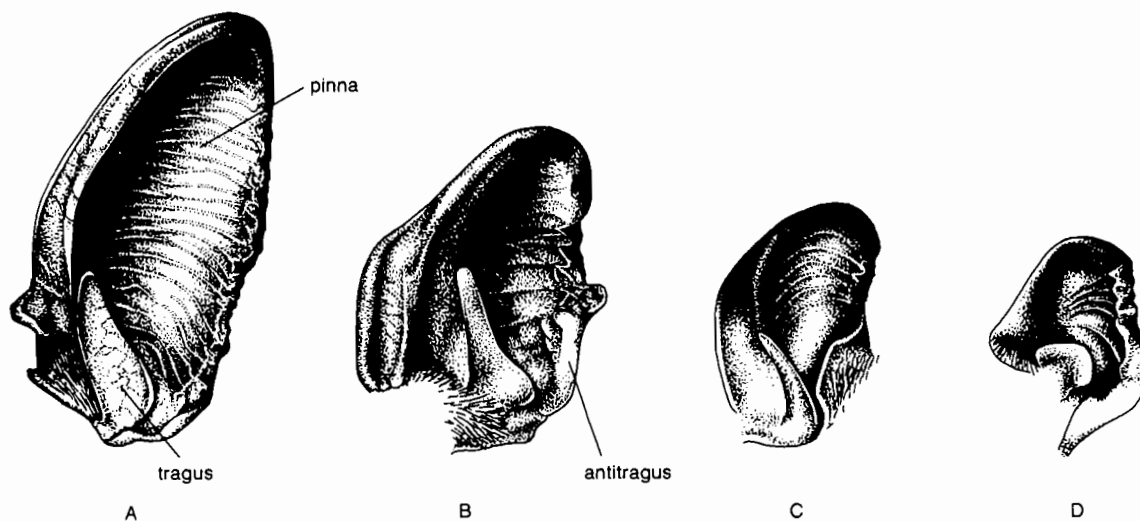
Fig. 2.5 *Variation of ear and associated structures. A, Long-eared bat* (Plecotus auritus); *B, Barbastelle* (Barbastella barbastellus); *C, Daubenton's bat* (Myotis daubentonii); *D, European noctule* (Nyctalus noctula) *(all Vespertilionidae).*

are presumed to provide structural support for the pinna. They may also be involved in collecting certain kinds or frequencies of sound. In addition, bands of hair in particular, and diagnostic patterns, may be found inside the ears of some microchiropterans. The function of these is not known.

Two other ear components are found in the Microchiroptera. The first of these is the tragus. Its presence or absence and size and shape are used in

the taxonomic identification and recognition of many species (Fig. 2.6). The tragus, sometimes called the 'earlet', corresponds to the small cartilaginous knob located just above the ear notch of the human ear. The tragus is absent in all megachiropterans. Among microchiropterans, it is absent in the Rhinolophidae and Hipposideridae and is quite small in the Molossidae. In other microchiropterans the tragus is moderately to well developed. The tragus of Tomes' Long-
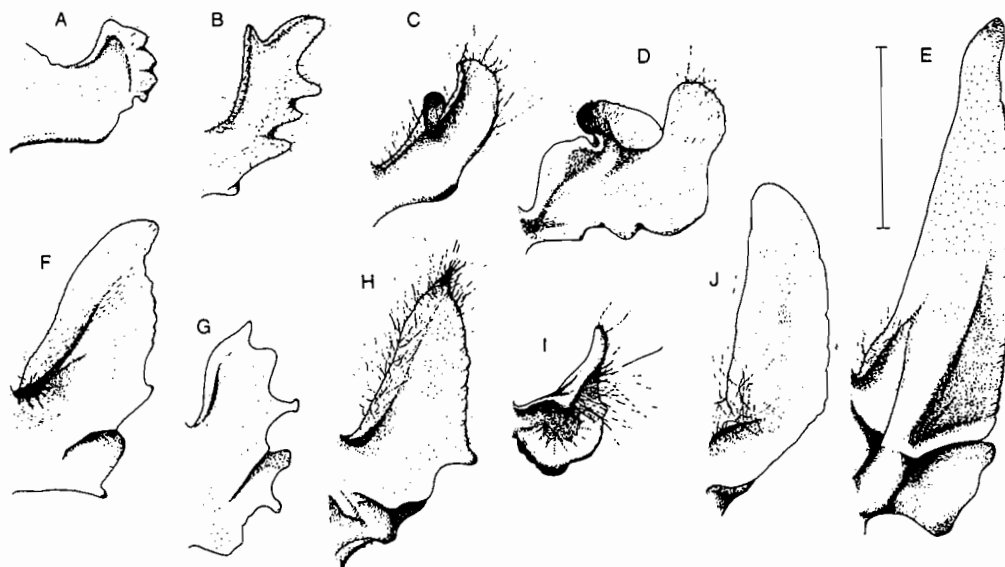

Fig. 2.6 *Tragus of some representative New World bats. A,* Saccopteryx bilineata *(Emballonuridae); B,* Noctilio albiventris *(Noctilionidae); C,* Pteronotus macleayii *(Mormoopidae); D,* Mormoops megalophylla *(Mormoopidae); E,* Lonchorhina aurita *(Phyllostomidae); F,* Carollia perspicillata *(Phyllostomidae); G,* Ametrida centurio *(Phyllostomidae); H,* Desmodus rotundus *(Phyllostomidae); I,* Natalus stramineus *(Natalidae); J,* Eptesicus fuscus *(Vespertilionidae). Line adjacent to E is 5 mm in length.*

eared bat (*Lonchorhina aurita*) is almost as long as the ear conch (Fig. 2.6E). The second ear component is the antitragus (Fig. 2.5) and its presence and shape are occasionally used for taxonomic purposes. There is no easily explained equivalent in the human ear, although it would be situated below the notch and just above the ear lobe. When present, the antitragus is a broad process or flap that is continuous with the outer margin of the pinna (Fig. 2.7). It is well developed in rhinolophids, hipposiderids, and molossids.

The range of variation in the size and shape of microchiropteran ears is almost as large as the number of species in this group. Relatively simple ears are found among the vespertilionids and some of the New World leaf-nosed bats (Phyllostomidae). The three small families of New World bats (Natalidae, Thyropteridae, and Furipteridae) have funnel-shaped ears with a short, generally blunt tragus. Craseonycterids, rhinopomatids, and emballonurids have simple but broadly rounded and cup-shaped ears; the tragus may be long and slender or short and broad. The ears of these bats are never connected, but there may be a short flap extending onto the forehead above the eyes.

The ears of horseshoe bats (Rhinolophidae) and Old World leaf-nosed bats (Hipposideridae) (Fig. 2.7) are similar in general appearance. The range of variation is great, with short (round or pointed) ears to large, broadly rounded, nearly funnel-shaped ears. The size of the ear conch may proportionately exceed the size of the head. The tragus is always small (scarcely more than a small knob deep inside the ear) or absent and the complexity of the ear may be augmented by a large, flap-like antitragus.

A number of microchiropterans have exceptionally long ears. Long ears are characteristic of three families: Nycteridae, Megadermatidae and Myzopodidae. Long-eared species also occur among the Phyllostomidae (*Lonchorhina*, *Tonatia*, *Chrotopterus*, *Macrotus*, and *Mimon*); Vespertilionidae (*Plecotus*, *Idionycteris*, *Euderma*, *Histiotus*, *Otonycteris*, *Antrozous*, and *Nyctophilus*); and Molossidae (several species of *Eumops*). The long ears of megadermatids are always united for at least a third of their length from the base. The ears of most molossids, whether long or short, are usually connected by a strong band above the eyes. The ears of the Sucker-footed bat (*Myzopoda aurita*), from Madagascar, are exceptionally long and slender and not connected. In addition, the tragus is long and fused to the inner margin of the pinna. The antitragus is a peculiar mushroom-like pad that fills most of the space at the base of the ear conch.

The long ears of megadermatids, nycterids, myzo-

podids, and phyllostomids are structurally rigid and under normal circumstances stand erect above the head. Those of most of the long-eared vespertilionids are the same, but the long ears of the vespertilionid genera *Plecotus*, *Idionycteris*, and *Euderma* are peculiar in the following respect. While resting in the day roost or in temporary night roosts, these bats fold their long ears into tightly curled bundles on either side of the head. Actually, they deflate their ears by closing special valves in blood vessels that enter the ear conch, thereby allowing the ears to collapse. When these bats become active, the vascular valves leading into the conch are opened and in-rushing blood slowly unfurls the collapsed ear. In a few seconds, the ears are pumped up to their fully erect posture. The functional significance of this behaviour is not fully understood, but it is thought to be a means of reducing heat (and perhaps water) loss while the bat is at rest or in hibernation.

Unlike other bats with long ears that stand more or less perpendicular to the long axis of the head, the ears of molossid bats (both long and short) lie forward, nearly parallel to the long axis of the head and body. As we noted above, the inner margins of the ears are usually connected by a band of skin. The reason for this ear posture seems to be correlated with the swift flight of these bats and functional aerodynamic requirements operating on the shape of the head. These ears are structurally rigid and have thick cartilaginous margins that maintain their streamlined aerodynamic shape.

The eyes

Most bats (Microchiroptera) rely almost exclusively on acoustic orientation and, therefore, usually have rather small to minute eyes. The small size of most bats' eyes and the fact that they are often hidden in the fur of the face has led many people to the common notion that bats either have no eyes or they are necessarily blind. This misconception is far from true, although the degree to which visual orientation is utilized by bats is not well understood. Studies on the Pallid bat (*Antrozous pallidus*) clearly indicate that it has an exceptional ability to discriminate patterns, even in extremely low light situations. Experiments with point sources of light also suggest that the Big Brown bat (*Eptesicus fuscus*) should be able to see bright stars. Individuals of some cave-dwelling species become restless before it is dark outside and hover or mill about the cave entrance as though checking the level of light. Visual acuity may be important in recognizing landmarks among species that forage over long distances or for those species that migrate long distances seasonally. Among the

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Microchiroptera, only the members of the Phyllostomidae have large eyes and it is thought that they may rely more on visual acuity in their nightly activities. Two phyllostomid species, Seba's Short-tailed bat (*Carollia perspicillata*) and Geoffroy's Tail-less bat (*Anoura geoffroyi*), have been observed (experimentally) to recognize and discriminate patterns.

In sharp contrast to the Microchiroptera, the eyes of megachiropterans are exceptionally large. These bats unquestionably utilize visual orientation more than audition. The light-sensitive part of the eye, the retina, is uniquely constructed with an outer layer (choroid) with numerous papillae that project back into the retinal surface. This may increase the available retinal surface area and thereby enhance the visual acuity in low light conditions. Many (perhaps all) megachiropterans have a tapetum lucidum that causes the eyes to shine bright red in a spotlight. The use of vision is discussed in relationship to migration and homing in Chapter 9.

The nostrils

The external nares (nostrils) of bats are usually located at the apex of the muzzle or nose. Typically these are round and open to the side of the muzzle. In many species the nostrils may be incorporated into discrete narial pads as in the Hog-nosed bat (*Craseonycteris thonglongyai*) or the Mouse-tailed bats of the genus *Rhinopoma*. The latter inhabit arid regions of the Old World and the nostrils are slit-like rather than rounded or crescentic in shape and they are valvular. This may allow them to close the narial passage and thereby exclude the dust from their dry and sandy surroundings. In bats that have noseleaves, the nostrils are intricately incorporated into these integumental ornamentations and they usually open upward. Several bat species, notably the Tube-nosed fruit bats (*Nyctimene* and *Paranyctimene*–Pteropodidae) and the Tube-nosed bats (*Murina*–Vespertilionidae), have nostrils opening laterally at the ends of short tubes–hence the common name 'tube-nosed'. The Bulldog bat (*Noctilio leporinus*–Noctilionidae) and the New Zealand Short-tailed bat (*Mystacina tuberculata*–Mystacinidae) have nostrils opening from a short tubercle at the end of the muzzle.

Facial foliations

While the faces of many bats possess no other distinctive features than those described above, several families of bats have curious and prominent fleshy excrescences of skin ornamenting the face. These usually take the form of leaf-like appendages associated with the nose region and are generally referred to as noseleaves. Noseleaves are characteristic features of the Rhinolophidae, Hipposideridae, Megadermatidae, and Phyllostomidae. Although not closely related in terms of genealogy, the noseleaves of the families Megadermatidae and Phyllostomidae are similar in appearance. In these families, the single blade-like noseleaf arises from a fleshy plate that surrounds the nasal apertures and stands erect behind these openings. The noseleaves of these bats may be long or short, slender or broad. In the phyllostomid Long-eared bat (*Lonchorhina aurita*), the length of the noseleaf nearly equals the length of its extremely elongated ears. This is also the case in its close relative, the Long-legged bat (*Macrophyllum macrophyllum*). It is interesting to note that the scientific (generic) names of these two bats refer to the shape and size of the noseleaf, *Lonchorhina* meaning literally 'spear nose' and *Macrophyllum* 'large leaf.' In another phyllostomid (*Sphaeronycteris toxophyllum*) the species name perhaps reflects a falsely attributed poisonous quality of the noseleaf that may portray the supposedly sinister nature of this bat. In reality, this bat is a quite docile and contented fruit-eating species. In the true vampire bats (Phyllostomidae) the noseleaf has been greatly reduced and modified into a complex series of folds and bumps around the ornamented narial plate.

The noseleaves of the Rhinolophidae and Hipposideridae are much more complex than those described above (Fig. 2.7). In both of these families the nasal apertures are surrounded by a broad, U-shaped plate. The resemblance of this plate to a horseshoe has led to the common name 'Horseshoe bats' for the family Rhinolophidae. The hipposiderids are simply called the Old World leaf-nosed bats.

In the rhinolophids, there is a vertical projection (sella) from the centre of the horseshoe behind the nostrils (Fig. 2.7). Occasionally the sella may incorporate secondary flaps of skin at its base to form a cup-shaped structure overlying the nasal openings. Behind the sella is a large, usually pointed, leaf called the lancet, that bears a number of complex folds and pockets along its edges. The sella and lancet are joined by a connecting process that also may have a curious shape. In addition, the noseleaf of rhinolophids may have a distinctly arranged pattern of sensory hairs.

The noseleaf of hipposiderids, while similar in some respects to those of rhinolophids, is often more complex. In its simplest form, there are two leaves or flaps behind the narial openings (Fig. 2.7). The hindmost (posterior leaf) may have several deep, forward facing pockets. The intermediate leaf is located just behind the nostrils and may have swollen areas or finger-like projections on its dorsal border.
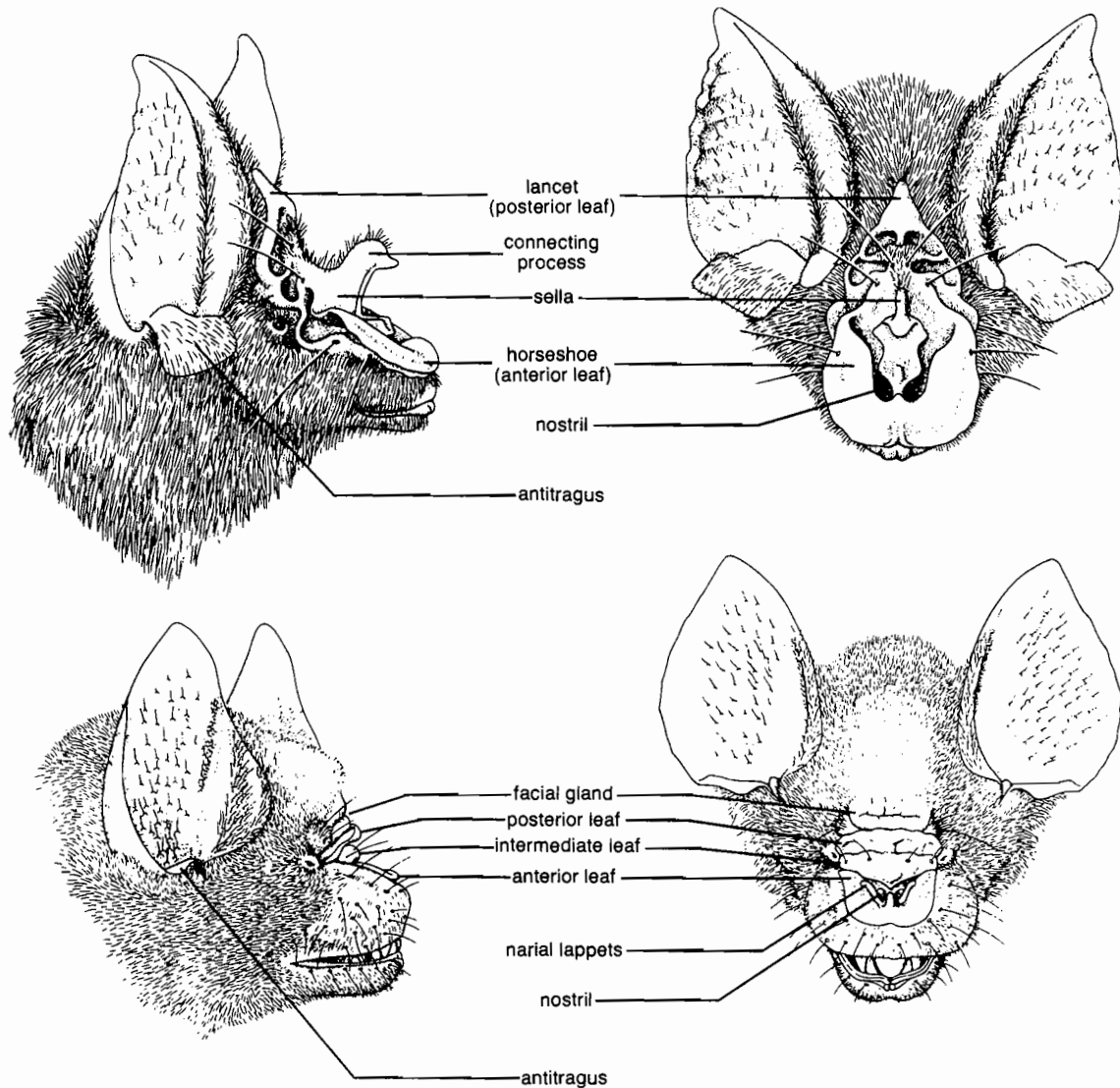
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Fig. 2.7 Noseleaf of Rhinolophus euryotis *(Rhinolophidae) (top) and* Hipposideros maggietaylorae *(Hipposideridae)*
(bottom).

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Additional complexity of the hipposiderid noseleaf may involve ornamental flaps around the nostrils, plate-like structures between the nostrils, and spikes, bumps, and complex folds on the dorsal margin of the posterior leaf. Several secondary leaflets occasionally occur under the antero-lateral edges of the horseshoe.

In some species of rhinolophids and hipposiderids, the structure of the noseleaf is truly bizarre. It is often used to characterize species or groups of species. The function of all noseleaves is not known, but they are thought to contribute to directing the acoustic orientation sounds that these bats produce.

Other facial foliations involve flaps and plates of skin not directly associated with the nose region. Notable examples are the bats of the family Mormoopidae (Moustached bats and Ghost-faced bats), in which the lips and chin regions are ornamented with complex foliations. These may function in directing the acoustic orientation sounds like a megaphone or they may augment the funnel shape of the mouth and thus facilitate the capture of insects as the bat flies through the air.

The bats of the family Nycteridae (Slit-faced bats) have a peculiar facial ornamentation. There is a

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longitudinal furrow or slit on the upper surface of the muzzle. In front of and on either side of this slit are noseleaf-like structures that may be extremely complex.

The Wrinkle-faced bat (*Centurio senex*) has, perhaps, the most bizarre and grotesque face of all bats (Fig. 2.8). It is a New World leaf-nosed bat adapted to feeding on fruit and has a much flattened, naked face. Being a phyllostomid, it has a noseleaf, but, in addition, its face is covered with a complex array of wart-like outgrowths, folds, and flaps. Even more peculiar is a deep chin fold which can be drawn over the face when the bat is at rest.
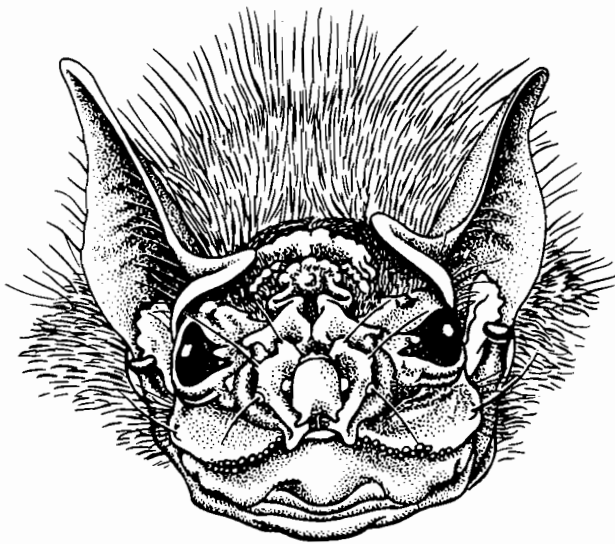
Fig. 2.8 *Facial ornamentation of the Wrinkle-faced bat* (Centurio senex–*Phyllostomidae*).

Finally, many bats have large fleshy lips that may contribute to facial ornamentation. In the Free-tailed bats (Molossidae) the lips are highly wrinkled, whereas in the Bulldog bats (*Noctilio*), the upper lips are large and covered with many small bumps.

Body size

While it is generally true that the bats of the suborder Megachiroptera are large and those of the Microchiroptera are small, there is considerable overlap in size. The largest bats *(Pteropus vampyrus* and *Acerodon jubatus)* are megachiropterans and have a wing span of nearly two metres. The smallest bat, *Craseonycteris thonglongyai*, is a microchiropteran and has a wing span of 130-145 mm. However, between these extremes we find *Macroglossus minimus* (Megachiroptera) with a wing span of 210-240 mm and *Vampyrum*

spectrum (Microchiroptera) with a wing span of almost a metre. Weights also reflect these differences in size. *Pteropus* weigh 500-1200 g and *Craseonycteris* tips the scales at about 2 g.

Body size of bats appears to be closely related to food habits and modes of flight. Physiological factors also play a part. Fruit-eating species are generally large in size as are carnivorous bats such as *Vampyrum spectrum* (Phyllostomidae) and *Macroderma gigas* (Megadermatidae). These large-sized species usually have long, broad wings and are capable of lifting heavy weights; flight speeds are relatively slow in these species. Large-sized species have an extra advantage over smaller species in that they have a relatively lower surface to volume ratio and do not lose body heat so rapidly.

Insect-eating bats are generally smaller than fruit-eating bats. Insects are highly dispersed in the environment and may be somewhat elusive; more than a few are required for a sufficiently energy-rich meal. Capturing insects on the wing requires fast and highly manoeuverable flight styles which themselves require high energy input. Thus, insectivorous bats must eat large quantities of insects on a regular basis; some experts estimate anywhere from one quarter to one half of their body weight nightly.

Body shape

Aerodynamic forces that occur during flight are a major factor determining body shape in bats as well as in other organisms that fly or glide. The bodies of bats are somewhat flattened and tapered from the shoulders to the hip region. The bulk of the weight is distributed in the upper chest region (centre of gravity) and is composed primarily of the heavy flight muscles. Bats utilize muscles located on the chest and back to operate their wings. In contrast, birds are deep-chested because all of their flight musculature is located in this ventral position. The breast bone of birds is strongly keeled to accommodate this mass of muscles. This bone is not markedly keeled in bats.

The hindlimb and foot

Much attention has been directed toward the modification of the forelimb (wing) of bats. However, the hindlimb has also undergone a number of changes associated with the flying ability of bats. For the most part, the hindlimbs have lost their function as locomotory appendages. This is not to say that bats are incapable of moving about on the ground; some are quite agile. Nonetheless, the hindlimb of bats is no longer a weight-bearing appendage such as that of a human leg. The most striking feature of the

hindlimb is that the upper leg bone (femur) has been rotated 180° from its normal position in other terrestrial mammals. Whereas the knee is directed forward in most other mammals, it is directed rearward (actually upward) in bats. Thus, the posture of the hindlimb of a bat at rest, on a flat surface, is rather spider-like. This curious limb posture has to do with the attachment of the wing membranes to the hindlimb as well as the attachment of the interfemoral membrane (uropatagium) and the co-ordinated control of these flight membranes. The bones of the leg, like those of the wing, are long and slender. Indeed they are longer and more slender than would be expected in a normal four-footed mammal of equal size and weight. They would, no doubt, break or bend if subjected to the weight-bearing stresses (compression) of a normal leg. However, bats do not walk, in the strict sense, on their legs; they hang suspended by them from a foothold in the roost. The weight-bearing forces of suspension (tension) are very different from those of compression. Imagine balancing a kilogram block on top of a dried strand of spaghetti; it would shatter under the compressive force. On the other hand, imagine suspending the same block from the strand of spaghetti; it would probably hold the weight. The same dynamic principles apply to a bat's leg. Indeed, the spider-like posture of the hindlimbs cradles (suspends) the body and is geared to reducing compressive stresses when bats move around on the ground. Species such as the Pallid bat (*Antrozous pallidus*) and the Common vampire (*Desmodus rotundus*) that frequently move about on the ground have slightly stouter leg bones than those species that do not.

The feet of bats are usually small. The toes are rather long and terminate with strong, sharp claws. In fish-eating species such as the Bulldog bat (*Noctilio leporinus*), Fishing bat (*Pizonyx vivesi*), and Kei myotis (*Myotis stalkeri*), the foot is unusually large and the toes are compressed laterally and terminate with a large sharp claw. These are adaptations for seizing and holding the prey.

The tendons in the legs and feet of bats are organized in such a way that the suspended weight of the hanging bat causes the toes and claws to grip the foothold in the roost firmly, even while the bat is sleeping (Fig. 2.9). A foot structure that allows an automatic grasping ability while at rest is also found in passerine (perching) birds. However, in these animals the anatomical arrangement is designed for an upright roosting posture.

Another structure that is associated with the foot and is unique to bats is the calcar (Fig. 2.1). This usually long cartilaginous structure articulates with the heel bone (calcaneum) and is bound in the
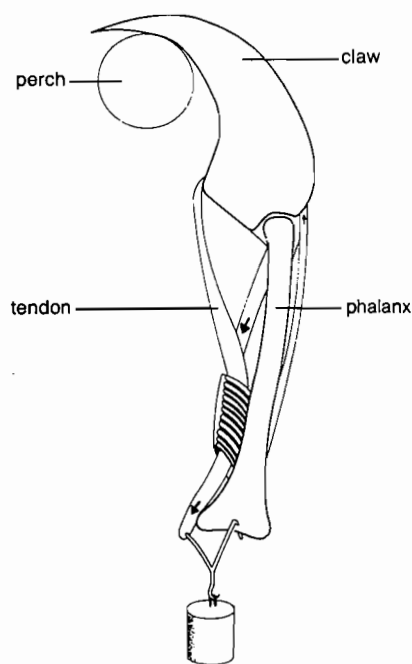

Fig. 2.9 A tendon in the foot helps to keep the claws firmly hooked to the perch by utilizing the weight of the hanging bat (After Schaffer, 1905).

uropatagium. Its function is to support the trailing edge of this interfemoral flight membrane and by muscular control it can be used to make camber changes in the uropatagium during flight. In the fishing species, it is usually very long and blade-like and serves to hold the posterior portion of the uropatagium out of the water as the bat is grasping its prey. The degree to which the calcar is developed in other species is variable and in many it may have a fleshy keel. These features are often used in the identification of particular species or groups of species. The Hog-nosed bat (*Craseonycteris thonglongyai*) and Mouse-tailed bats (Rhinopomatidae) do not have a calcar (Fig. 2.10E-F); it is knob-like in the vampires (Desmodontinae).

In a few species, there are peculiar sucker-like pads or discs attached to the side of the foot as well as the wrist region. These structures facilitate the curious roosting behaviour of these species which usually involves seeking shelter inside the rolled leaves of bananas and other similar plants. In the African Banana bat (*Pipistrellus nanus*–Vespertilionidae) there is a slightly developed pad on the palmar surface of the wrist; they lack a sucker on the foot. There is a moderately well-developed adhesive pad on the wrists and feet of the Club-footed bats (*Tylonycteris*) and Thick-thumbed pipistrelles (*Glischropus*). Similar
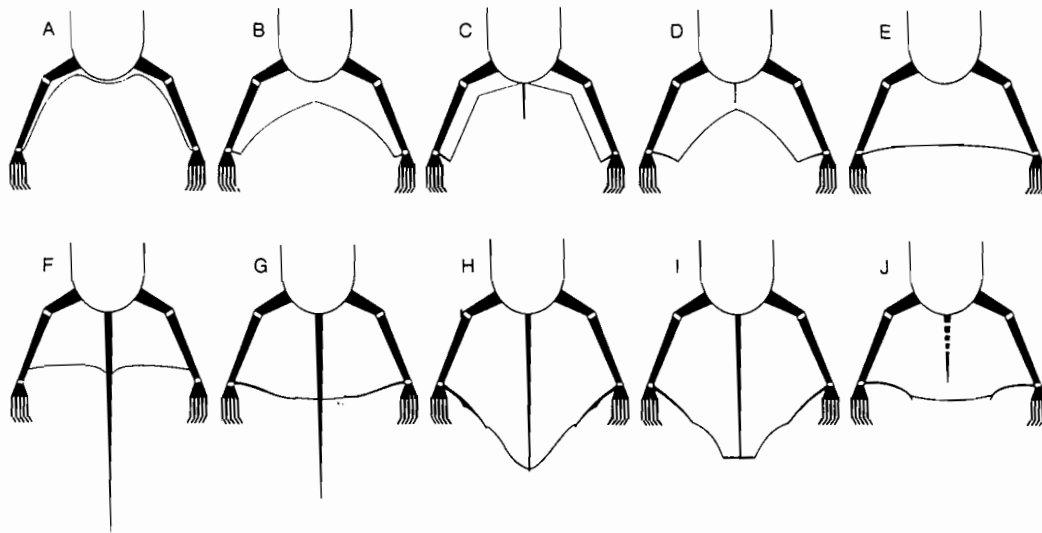
Fig. 2.10 *Tail and uropatagium of bats. See text for discussion.*

adaptations are found in the Disc-footed bat (*Eudiscopus denticulus*) and in *Myotis rosseti*. All four of the aforementioned species are members of the Vespertilionidae and live in southeastern Asia. The most highly developed sucker-discs are found in the Sucker-footed bat (*Myzopoda aurita*–Myzopodidae) of Madagascar and the New World Disc-winged bats (*Thyroptera*–Thyropteridae).

The tail and interfemoral membrane

Nearly all bats have a tail, although like many of the structures discussed above, there is considerable variation. The Mouse-tailed bats (*Rhinopoma*) are so named for their long, free tail (Fig. 2.10F). By 'free-tailed' we mean that the tail or some substantial portion of it is not bound in the interfemoral membrane and trails freely behind the bat. In rhinopomatids the tail is very long and thread-like and not as thick as a mouse's tail. The bats of the family Molossidae are all characterized by having at least half of the tail protruding from the rear margin of the uropatagium (Fig. 2.10G). Indeed, they are called Free-tailed bats. A long, free tail is found in the Long-tailed fruit bat (*Notopteris macdonaldi*–Pteropodidae) which is found in the New Hebrides (Vanuatu), New Caledonia, and Fiji. This pteropodid, as well as members of the family Rhinopomatidae are thought by some bat biologists to be very primitive because of their long tails since it is supposed that the ancestors of bats had long, free tails. While this may or may not be true, these long-tailed species do not appear to be as primitive or as ancestral as many

would desire. Long tails are a general characteristic of the Evening bats (Vespertilionidae). Their tails, however, are completely (or nearly so) bound within the uropatagium (Fig. 2.10H). Similar conditions are found in the Rhinolophidae, Hipposideridae, and Megadermatidae (tail may be absent in some). The tail of nycterids is also long and enclosed in the uropatagium. In addition, there is usually a T- or Y-shaped cartilage at the tip of the tail (Fig. 2.10I). In three families (Emballonuridae, Noctilionidae, and Mormoopidae), the tail protrudes for about 10-15 mm from the top surface of the interfemoral membrane at about the level of the knee (Fig. 2.10J). These bats have moderately well-developed calcars and these help fold the posterior, tail-less portion of the uropatagium forward under the anterior portion of the uropatagium. In this posture, these bats appear to have a 'free tail.'

The tail may be short or absent in some species. *Craseonycteris thonglongyai* is peculiar because it has an extensive uropatagium but lacks any remnant of a tail or calcars (Fig. 2.10E). This is odd because a reduction in the length of the tail is usually accompanied by a similar reduction in the expanse of the uropatagium.

Most pteropodids do not have tails or much of an interfemoral membrane. Short, free tails are found in the rousettes (*Rousettus*) and the Tube-nosed fruit bats (*Nyctimene* and *Paranyctimene*–Fig. 2.10C). Within the New World leaf-nosed bats (Phyllostomidae) there is considerable variation relative to the length of the tail and the form of the uropatagium (Fig. 2.10A-B, D).

Hair

Hair is a unique characteristic of mammals and the bodies of nearly all bats are covered with a coat of hair or fur. Hair consists of dead epidermal cells that contain keratin, a tough, flexible substance made of proteins. Keratin is also found in nails and claws. The hair filament, although dead, grows from living cells located in special bulb-shaped structures called hair follicles at the root of each hair in the epidermis of the skin.

Each hair consists of three distinct, microscopic regions. The centre of a hair is called the medulla and, in most mammals it contains air spaces and colour pigments. The hairs of vespertilionids lack a medulla. In addition, the medulla is absent in some species of the Emballonuridae, Nycteridae, Rhinolophidae, Hipposideridae, Noctilionidae, Phyllostomidae, Natalidae, Thyropteridae, Myzopodidae, Mystacinidae, and Molossidae. Nearly all megachiropterans (Pteropodidae) have a medulla as do megadermatids. When present, the medulla is usually fragmented; that is, it appears as a string of beads running through the core of the hair. The bulk of the hair is made up of the cortex. This region may also contain colour pigments and in most bats the cortex accounts for the overall coloration of the fur. The outside of the hair filament is covered with many flat scale-like cells called cuticular or coronal scales. These scales often have distinctive shapes and features that may be seen only under very high magnification such as provided by the scanning electron microscope (Fig. 2.11). These scales may be closely appressed to the hair shaft (Fig. 2.11A, F) or they may be divergent (Fig. 2.11B-E, G). In addition, their margins may be smooth or entire (Fig. 2.11A-B, F), mildly crenulate (saw-toothed as in Fig. 2.11G), or strongly denticulate (Fig. 2.11C, E). The characteristics of coronal scales have been used by some to identify species or groups of species. However, the effort and expense required to see them often makes them difficult to study. There is no apparent correlation between the structure of the coronal scales and the habits of bats.

The coat of hair is called fur or pelage and it functions primarily as insulation. The pelage of most mammals may be divided into several different kinds of hairs. The most prominent of these are the underfur (fine and very dense) and the overfur or guard hairs (usually long and coarse). In most bats, there is little or no distinction between these two kinds of hairs. In fact, the pelage of most bats is rather uniform in length and overall density. Some vespertilionids may have distinct guard hairs with the outer third of the hair filament somewhat expanded.
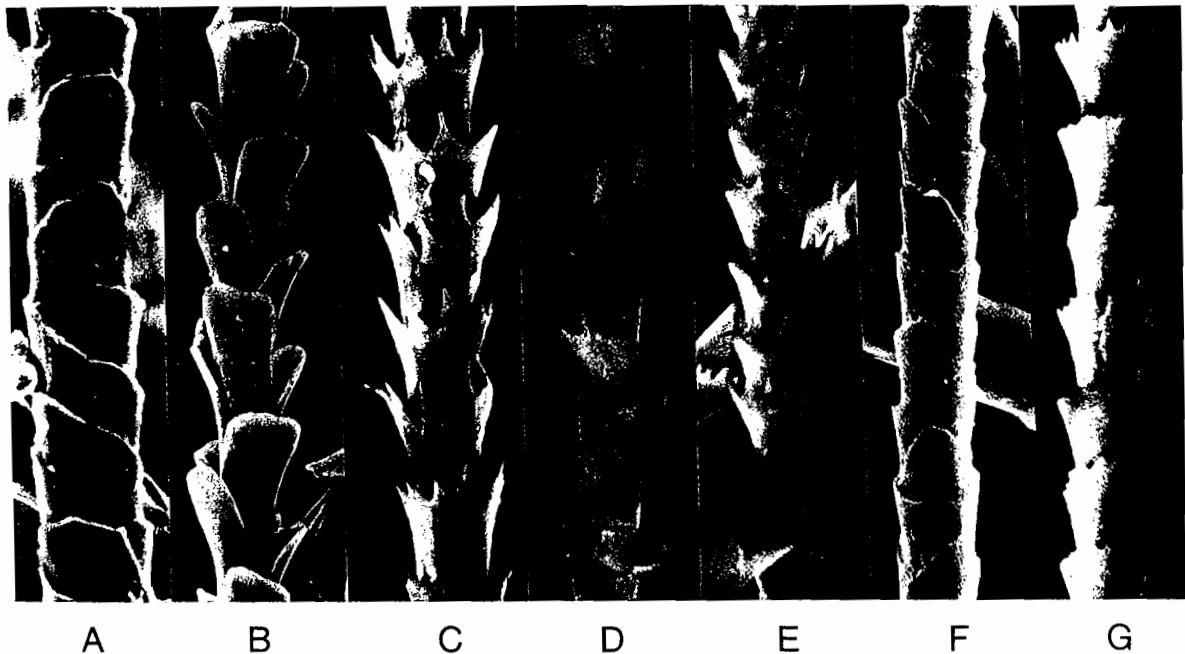

Fig. 2.11 Scanning electro-micrographs of cuticular (coronal) scales of bat hair. A, Macroglossus sobrinus (Pteropodidae); B, Epomophorus anurus (Pteropodidae); C, Rhinopoma hardwickei (Rhinopomatidae); D, Emballonura nigrescens (Emballonuridae); E, Mormoops megalophylla (Mormoopidae); F, Natalus stramineus (Natalidae); G, Eumops perotis (Molossidae). Scale approx. × 1000.

The length of the pelage of bats varies from 3-4 mm in some vespertilionids and molossids to 40 mm in *Acerodon* (Pteropodidae). Species that roost in outdoor situations such as trees often have very dense and moderately long fur. Short but frequently dense fur is found on most cave-dwelling species. The pelage may be sparse and coarse in tropical species or those that inhabit arid or semi-arid regions. The greatest variation in the nature of the pelage may be found in the Megachiroptera. Among microchiropterans, extremely woolly (underfur) pelages are found in such species as the Woolly False vampire (*Chrotopterus auritus*–Phyllostomidae), Commerson's leaf-nosed bat (*Hipposideros commersoni*–Hipposideridae), Lesser Woolly Horseshoe bat (*Rhinolophus sedulus*–Rhinolophidae), and Woolly bats of the genus *Kerivoula* (Vespertilionidae). These long, woolly coats are exceptional, perhaps because they are difficult to dry. The pelage of some vespertilionids and most molossids is very short and silky. In the latter, fresh pelage may have a glossy sheen or lustre.

There is only one naked bat, the Hairless bat (*Cheiromeles torquatus*–Molossidae). The Bare-backed fruit bats (*Dobsonia*–Pteropodidae) and the Naked-backed bats (*Pteronotus davyi* and *P. gymnonotus*–Mormoopidae) have backs that appear to be nude. However, these bats are not truly naked-backed. The naked skin is the fused wing membranes that meet on the midline of the back; beneath them is the normally furred back.

The length and texture of the pelage may play an important role in aerodynamically contouring or smoothing the body surface of bats. Many of the swift-flying species tend to have moderately short to close-cropped fur and the individual hairs are often very fine. In the genus *Pteropus*, the fur on different parts of the body may differ in length and texture. Often these bats have a collar (mantle) of woolly fur on the neck and shoulder region and short sparse fur on the back. The rump area may be clothed with fur similar to that on the back or it may be somewhat longer and more woolly.

Specialized patches or bands of hair are found in some species of bats. These patches are often more highly developed in males of the species. Males of the pteropodid genera *Rousettus*, *Myonycteris*, and *Megaloglossus* often have a collar or 'ruff' of coarse specialized hairs extending across the upper chest between the shoulders. White tufts of specialized hairs are found on the shoulders of the Epauletted bats (*Epomops* and *Epomophorus*–Pteropodidae). These specialized patches of hair are usually associated with skin glands and together they may function in male territorial behaviour and/or sex recognition. Brush-like clumps of stiff hairs are sometimes found

protruding from the centre of the facial gland (Fig. 2.7) in males of the genus *Hipposideros* or from the gular sac of the molossid genus *Platymops*. Other molossids have an erectile crest of hairs on top of the head that develops during the reproductive season.

Specialized hairs also include those with a sensory or tactile function. These are whisker-like hairs found on the muzzle or other facial regions. The noseleaves of the rhinolophids and hipposiderids often have a distinct pattern of tactile hairs (Fig. 2.7). Sensory hairs are also found on the tip of the tail or on the uropatagium. In the Molossidae, there are special spoon-shaped tactile hairs on the outer and inner toes of the foot.

Since hair is non-living, it is susceptible to wear and bleaching. Thus, it is replaced periodically by a process called moulting. Whereas other mammals may have two moults in a year, bats appear to moult only once a year. This is usually accomplished in late spring by males and non-reproducing females. Reproductive females delay moulting until after the young are weaned and lactation ceases. Brown and reddish-orange colour phases have been reported in some species of bats. However, in most cases, the brown individuals are males and/or non-reproductive females with fresh new pelage and the reddish individuals are lactating females with old bleached pelage.

In adult bats the annual moult usually follows a specific pattern (Fig. 2.12). On the back, moult centres first appear on top of the head, shoulder region, and on the rump. On the venter, moult usually starts as a band on the throat. From these initial centres, the moult spreads and progresses to all parts of the body. At first, this involves vascularization of the skin, but soon new hair growth begins. In other mammals, the new coat of hair is usually well developed before the old hair starts to fall out or is sloughed off in patches. In the few bats that have been studied, the old hairs apparently drop out as new hairs grow into place. Thus, there is usually no outward sign that the bat is moulting. This, too, has contributed to the confusion concerning colour phases in bats. In a population there may appear to be a brown phase and a red phase, with no apparent moult. However, in most of the species with reported colour phases, individuals have been discovered with old red hairs and new brown ones.

Coloration

Unlike ornately coloured birds and insects that rely on visual perception of colour and nuances of colour patterns in their social behaviour, bats do not appear
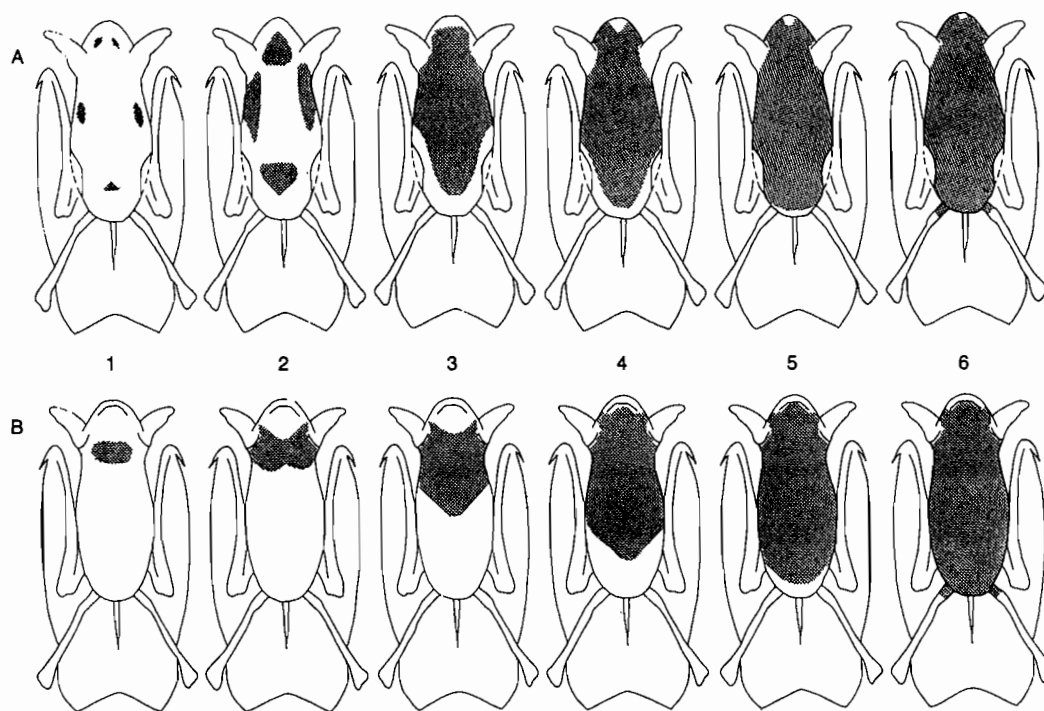
Fig. 2.12 *Generalized diagram of moult progression in* Pteronotus parnellii *(Mormoopidae). The dorsal views (A) and ventral views (B) depict moult progression (shaded area—stages 1–6) from left to right.*

to use these features in their social organization or individual discrimination. Striking colours and colour patterns are uncommon among bats and they are mostly varying shades of brown and grey. Although uncommon, some bats do have very striking and attractive colours and colour patterns. Many of these bat species roost outdoors in trees or other exposed shelters. Bats that inhabit arid to semi-arid regions tend to be pale in colour, whereas species from humid tropical and subtropical regions tend to be darker in colour. We have already commented on the colourful pigmentation that may be found in the flight membranes.

The overall colour or hue of the fur is determined by the genetically controlled distribution of colour pigments in the medulla or cortex of the hair. These pigments are usually distributed in bands of colour along the strand and there may be as many as three, perhaps more, such bands on any one hair. The individual hair filaments of drably coloured bats are usually monocoloured or bicoloured with light or dark bases and black or brownish tips. The coloration of some species may be enhanced by a lighter coloured band(s) either at the base of the hair filament or somewhere along the hair shaft. Depending on the intensity and extent of dark and light bands on such hairs, the overall colour of the fur may be pale or

appear mottled or multicoloured. Some species such as the vespertilionid Hoary bat (*Lasiurus cinereus*) and the Silver-haired bat (*Lasionycteris noctivagans*) have a white frosting on the fur that gives it an attractive grizzled or hoary appearance. This frosted effect occurs when monocoloured white or white-tipped hairs are scattered among the other coloured hairs of the fur. Whereas most mammals have pale coloured bellies, often in sharp contrast to the colour of the back, bats usually are uniformly coloured. Their bellies may be somewhat paler than the dorsal coloration.

In contrast to the norm among bats a few are white or nearly white. These include the Ghost bat (*Diclidurus virgo*–Emballonuridae) and the White bat (*Ectophylla alba*–Phyllostomidae); both inhabit the tropics of the New World. In addition, both of these bats combine yellowish pigmentation on the ears or other membranes for a distinctive general appearance. Neither species is albinistic and true albinism has been reported only rarely in bats. Likewise, all black or melanistic individuals are rare among bats.

Some species of New World leaf-nosed bats such as *Uroderma bilobatum*, *Vampyrops helleri*, and *Chiroderma salvini*, have a single white stripe extending from the back of the head, down the centre of the back, to the rump. The White-lined bats of the New
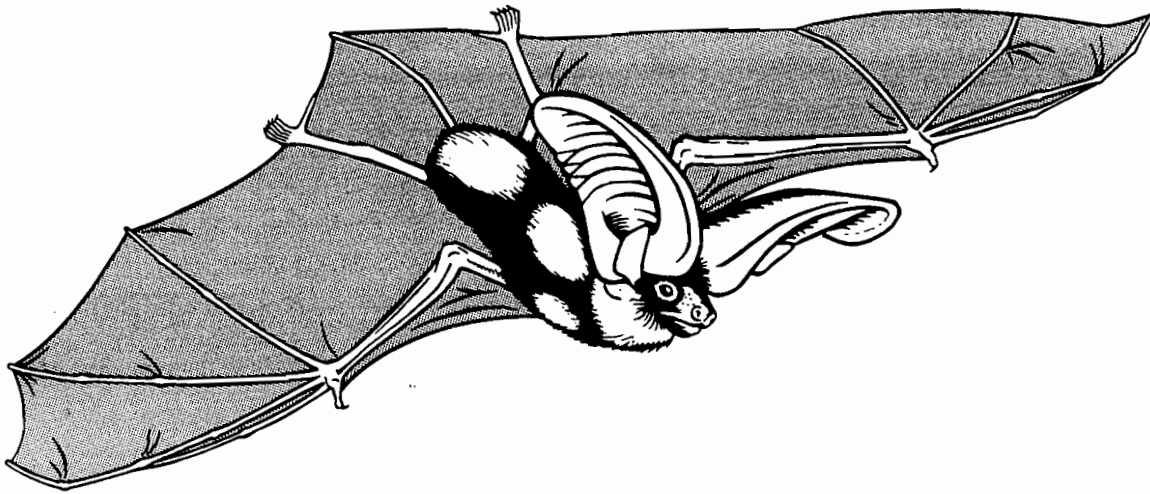
Fig. 2.13 *North American Spotted bat* (Euderma maculatum–*Vespertilionidae). Also note large ears.*

World emballonurid genus *Saccopteryx* have a pair of white stripes on the back. A light to dark black stripe is found on some species of Tube-nosed fruit bats (*Nyctimene*). In the Broad-striped Tube-nosed bat (*Nyctimene aello*), that lives in Papua New Guinea, this stripe has been expanded into a 15-20 mm wide black band. In contrast, the Big-eared Free-tailed bat (*Tadarida lobata*), a molossid from Kenya and Zimbabwe, has a small white interscapular spot, and white shoulder spots or patches of specialized hair (epaulettes) are found in some phyllostomids and among epomophorine pteropodids.

Among the most attractively coloured bats are those that have pure white spots, stripes, and/or a combination of these on jet black fur. The North American Spotted bat (*Euderma maculatum*) is one such species (Fig. 2.13). It has three large white spots arranged in a triangular pattern on the back. Its long, pale pink-coloured ears and pale flight membranes add to the contrasting colour pattern of this desert bat. The African Pied bat (*Glauconycteris superba*) has a similar colour pattern of white spots and bars on a black background. Indeed, nearly all species of the vespertilionid genera *Glauconycteris* and *Chalinolobus* have extraordinarily attractive colour patterns.

INTERNAL FORM

Skeletal system

The development of flight is undoubtedly the most important evolutionary innovation acquired by bats. Not unexpectedly, many of the adaptive features related to this unique mode of locomotion are reflected in the structure and organization of the skeletal system (Fig. 2.14). We have previously discussed many of these adaptations as they relate to the structure of the appendicular skeleton (wing and hindlimb). The axial skeleton (cranium, vertebral column, ribs, sternum, and pelvis) also reflects flight adaptations as well as other specializations unique to bats. Overall, the major modification to the chiropteran skeletal system involves the reduction in size and thickness of skeletal elements and the promotion of a sturdy yet lightweight support system.

The size and shape of the cranium varies widely among the many species of bats (Fig. 2.15). Its form is more directly related to food habits and feeding styles than to specific modifications for flight.

Perhaps the most obvious feature of the cranium is the dentition. Bats, like most other mammals, have a fully differentiated set of teeth. These include: incisors (front teeth), canines, premolars, and molars. All except the molars are deciduous; that is, they are replaced once in the life span of the individual. The deciduous teeth are often called milk teeth because these are the first teeth that suckling young acquire. In most mammals, the milk teeth are more or less similar in appearance to the permanent teeth which replace them sometime at or near adulthood. In bats, these teeth are highly specialized and unique in form. They are tiny, sharp-pointed, and hooked spicules that erupt in the mouth of young bats either prior to birth or very shortly thereafter. These specialized teeth enable the young bat to cling more effectively to the teat of its mother while she is carrying her offspring in flight. The claws on the feet and thumbs are also well-developed at this time. As the young bat
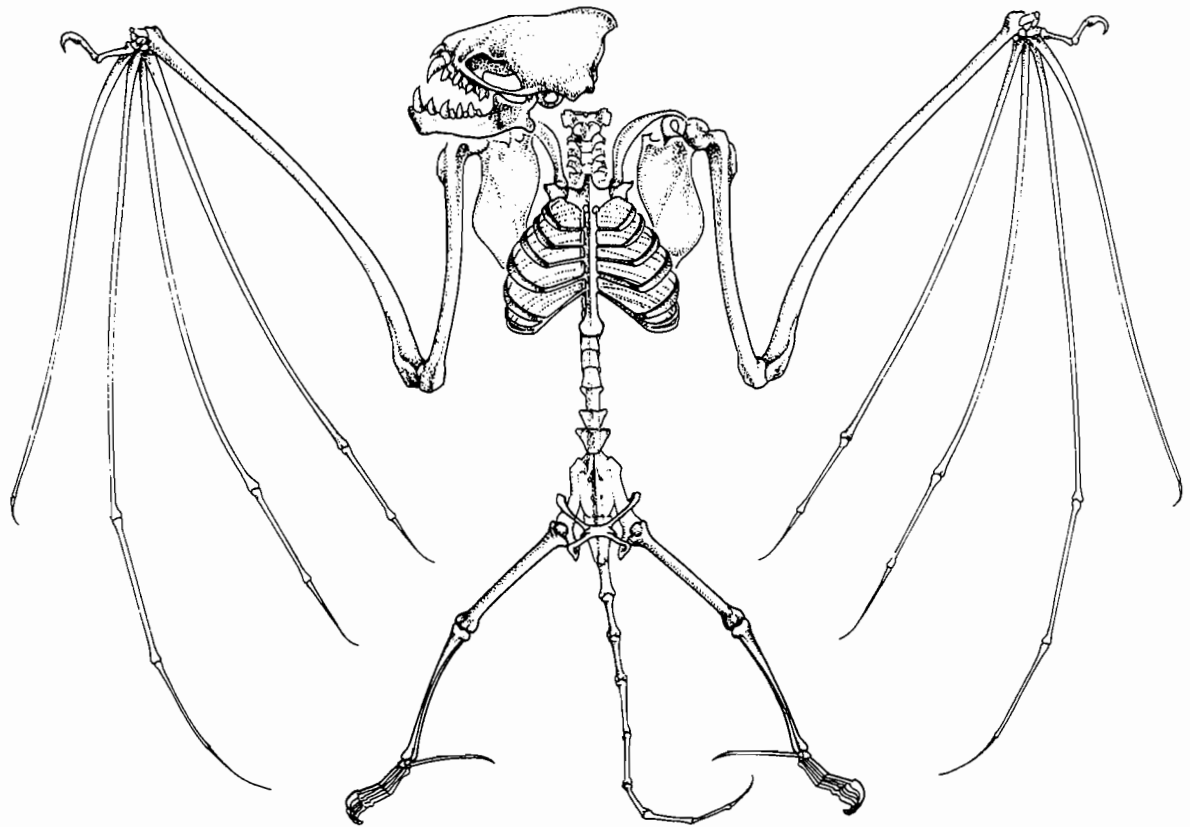
Fig. 2.14 Bat skeleton.

matures and is able to survive on its own, the milk teeth are replaced by the permanent dentition.

The basic or primitive number of teeth for placental (eutherian) mammals is 44. These are: three upper and lower incisors (I), one upper and lower canine (C), four upper and lower premolars (P), and three upper and lower molars (M). This representation includes a count of only one side (one-half) of the dentition and, thus, must be doubled to account for all teeth in both upper and lower jaws. The number of teeth found in a particular species or group of species is usually written as an abbreviated notation called the dental formùla. The dental formula for the primitive eutherian mentioned above would be: I 3/3, C 1/1, P 4/4, M 3/3 = 44. The largest number of teeth found in bats is 38. This means that bats are specialized compared to primitive mammals by having lost six teeth. This reduced dental formula is illustrated by the vespertilionid genus *Myotis* with: I 2/3, C 1/1, P 3/3, M 3/3 = 38. Note that one upper incisor and one upper and lower premolar are absent. The fewest number of teeth found in any bat is 20. This occurs in the Common vampire (*Desmodus*

rotundus) with: I 1/2, C 1/1, P 1/2, M 1/1 = 20. Again, notice that two upper and one lower incisors, three upper and two lower premolars, and two upper and lower molars are lost. Another interesting variation in dental reduction is shown by the Tube-nosed fruit bats (*Nyctimene*) with: I 1/0, C 1/1, P 3/3, M 1/2 = 24. Notice the complete loss of lower incisors and nearly complete loss of upper molars. There are over 50 dental formulae for bats, which highlights their wide diversity of dental adaptation. These modifications always involve incisors, premolars, and/or molars; all bats have a full complement of canines. As might be expected, there are many intermediate dental formulae and there are also many possible ways to acquire the same number, but different complements of teeth. For example, 30 teeth is a common number, but it is accomplished in 13 different ways. Related genera and families of bats tend to have similar patterns of tooth loss. The amount of dental variation in bats far exceeds that of all other groups of mammals. On occasion there is also some individual variation in the number of teeth. Among Old World fruit bats, for example, the Blossom bat (*Syconycteris australis*) may
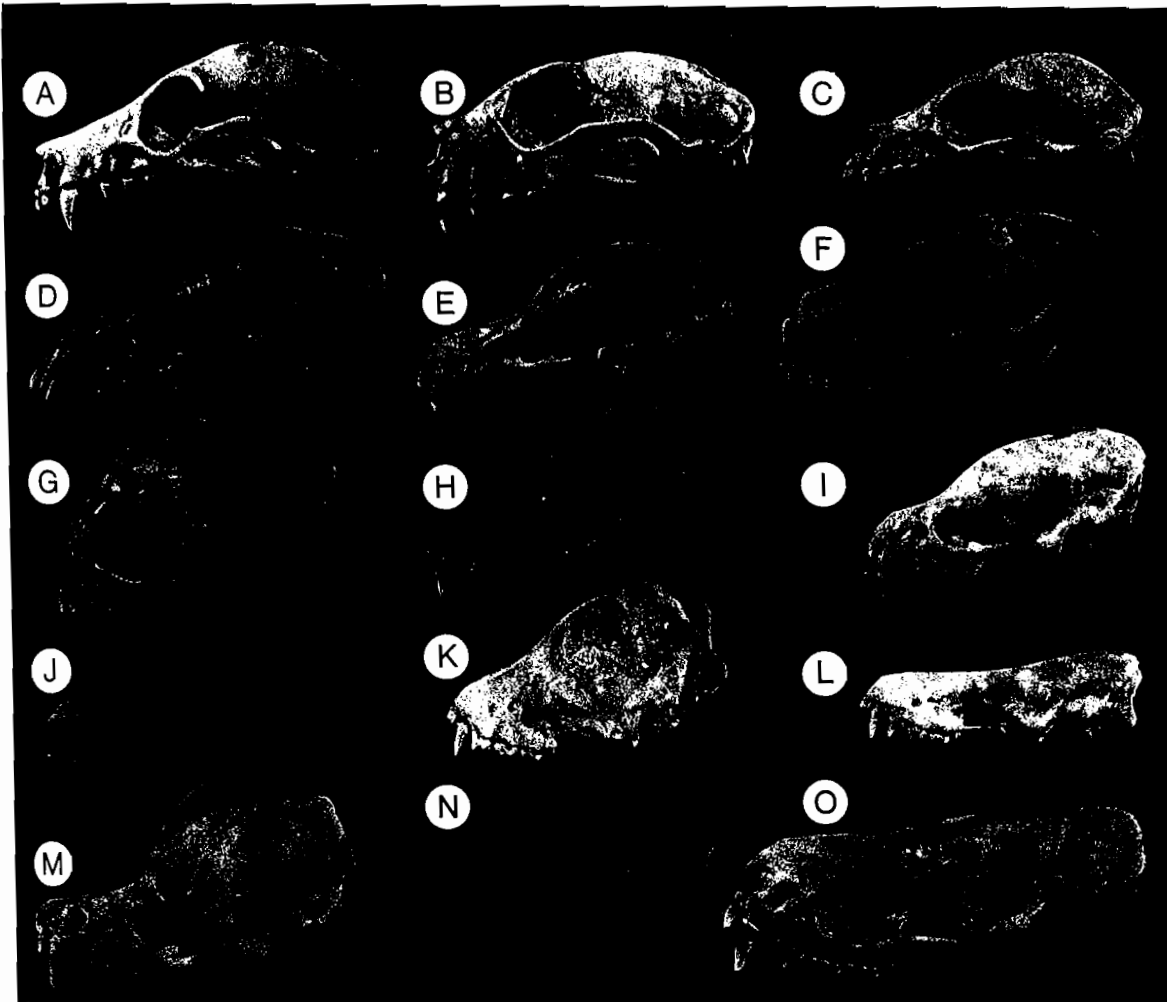
Fig. 2.15 Variation in the shape of the cranium. A, Melonycteris melanops *(Pteropodidae); B,* Nyctimene major *(Pteropodidae); C,* Syconycteris australis *(Pteropodidae); D,* Macrotus californicus *(Phyllostomidae); E,* Erophylla sezekorni *(Phyllostomidae); F,* Uroderma bilobatum *(Phyllostomidae); G,* Centurio senex *(Phyllostomidae); H,* Natalus stramineus *(Natalidae); I,* Pipistrellus angulatus *(Vespertilionidae); J,* Antrozous pallidus *(Vespertilionidae); K,* Nyctophilus microtis *(Vespertilionidae); L,* Tylonycteris pachypus *(Vespertilionidae); M,* Miniopterus tristis *(Vespertilionidae); N,* Molossus ater *(Molossidae); O,* Eumops perotis *(Molossidae).*

have four or five cheek teeth (premolars and molars) in the upper jaw and five, six or seven lower cheek teeth, while Anchieta's fruit bat (*Plerotes anchietae*) has similarly four or five upper cheek teeth but five or six in the lower jaw. Additionally, one pair of the usual four lower incisors of this species may be missing. In microchiropterans the tiny anterior upper premolar normally found in the vespertilionid genus *Pipistrellus* may be absent, while in the closely related genus *Eptesicus* the reverse may occur. In another vespertilionid genus, *Myotis*, the absence of the small second premolars may vary among individuals or in some cases is apparently characteristic of the species.

As in *Pipistrellus* there may be rarely a small supernumerary premolar crowded into the toothrow. Other aspects of the dentition will be discussed in Chapter 4.

Another variable aspect of the cranium is the size and shape of the braincase which directly reflects the size and shape of the brain (Fig. 2.15). Studies on mammals have shown that brain size is generally a direct function of body size. Thus, the size of the braincase, and the head in general, reflects the overall size of the body of the bat. The primary function of the braincase is to protect the brain from possible injury. Since it is also the site of attachment for the

temporal muscles which are involved in closing the jaws and chewing of food, its relative surface area is also an important consideration. Frequently, a prominent flange-like sagittal crest may be present on the dorsal midline of the cranium (Figs. 2.15M-N and 2.16A-C). Such a crest is present as a low to moderately well developed blade in many species. It is especially well developed in carnivorous or fish-eating bats or other large-sized bats that eat large beetles. A similar, but transverse lambdoid crest may be present on the rear portion of the braincase. Both of these crests provide an increase in surface area for the attachment of the temporal muscles. Occasionally, both sagittal and lambdoid crests may be drawn posteriorly past the rear margin of the braincase. This causes some fibres of the temporal muscles to be longer which consequently lengthens the effective lever arm of the jaw and provides a more forceful bite. The Hairless bat (*Cheiromeles torquatus*), the American False vampire (*Vampyrum spectrum*), and some large-sized species of Tomb bats (*Taphozous*) have such an arrangement in addition to heavy jaws. These are both features of a powerful biting mechanism (Fig. 2.16A-B, E). It is interesting to note in passing that similar crests are found in lions and tigers as well as many other large, powerful carnivores. In the vampire bats, the cranium is smooth and lacks any crests (Fig. 2.16D) but it is inflated and highly arched giving it the same general appearance as the carnivorous species just mentioned. This provides for the attachment and lengthening of the temporal muscles whose biting force is thereby focused on the blade-like canines and incisors.

Another departure from the normal shape of the braincase occurs among some species of Old World fruit bats (Pteropodidae) and, to a lesser extent, in some New World leaf-nosed bats (Phyllostomidae). In these, the braincase is deflected (bent) downward, often at a marked angle from the longitudinal axis of the skull (Fig. 2.15A). The most extreme cases of this deflection are found in the Pteropodidae. This has the same effect of lengthening some of the fibres of the temporal muscle. In this case, however, the force of the bite is not focused near the front of the mouth (at or near the canines), but is concentrated on the grinding teeth (molars).

The zygomatic arches are another component of the chiropteran cranium which may also reflect feeding adaptations. Typically, these are thin bars of bone that form an arc from just above the last upper molar tooth to a point just in front of and above the ear region (Figs. 2.15 and 2.16). In humans, this is called the cheek bone. The zygomatic arches serve as the attachment sites for the masseteric (chewing) muscles. These arches may be extremely fine and filamen-tous or even partially absent in some of the small delicate insectivorous species (Fig. 2.15D-E, L). In large bats that capture and chew hard-bodied insects such as beetles, or in some fruit-eating species, these bones are stout and well developed. They may be arched upward or widely flared, in either case lengthening the effective lever arm of the muscles they support. Occasionally they may have large flanges that provide additional surface area for the attachment of the masseteric muscles (Fig. 2.16C-D, G).

The lower jaws of bats also express a variety of forms depending on the food habits of a particular species. The length of the lower jaw may reflect the degree to which the dentition has been reduced. Long jaws generally have more teeth, whereas shorter jaws have fewer teeth. This is not entirely true, however, as pteropodids have generally long jaws but the teeth are often widely spaced along the length (Figs. 2.15A and 2.16G). In the nectar-eating phyllostomids (Glossophaginae) the jaws are quite elongated and the teeth are reduced both in size and number. This is also true in the nectar-eating pteropodids (Macroglossinae). The depth of the jaw ramus varies widely depending on the hardness or coarseness of food items. Thin and long-jawed species usually eat soft-bodied insects (flies and moths) or they may eat nectar or pollen (Fig. 2.16F-G). Short and thick-jawed species usually eat hard-bodied insects or vertebrate prey or they may eat tough-skinned or coarse, pulpy fruits (Fig. 2.16A-C, E). The jaw of the vampire (Fig. 2.16D) is also quite stout as it must bear the force of inflicting a substantial wound.

The rostral portion of the cranium is usually moderately long and pointed in most bats (Fig. 2.17A-B). In these the toothrows usually are attenuated (pointed) anteriorly. This is thought to be the primitive condition for bats. In the Old World fruit bats (Pteropodidae) there appears to be a trend toward shortening the rostrum. Short 'pugged' noses are found in the Dog-faced fruit bats (*Cynopterus*), Short-nosed fruit bats (*Penthetor lucasi*), and the Tube-nosed fruit bats (*Nyctimene* and *Paranyctimene*). In the microchiropteran family Emballonuridae, the rostral region is usually short and broad. In addition, sinuses in the rostral portion of the maxillary bone may be greatly inflated, thus further contributing to the broadening of the nose region. In the genus *Cheiromeles* (Molossidae), the nose is short (Figs. 2.16A and 2.17C) and straight-sided; the toothrows are only slightly attenuated anteriorly. The highest degree of facial shortening occurs among the fruit-eating leaf-nosed bats (Phyllostomidae) of the subfamily Stenodermatinae. Of these, the Wrinkle-faced bat (*Centurio senex*) is the most extreme (Figs. 2.15G
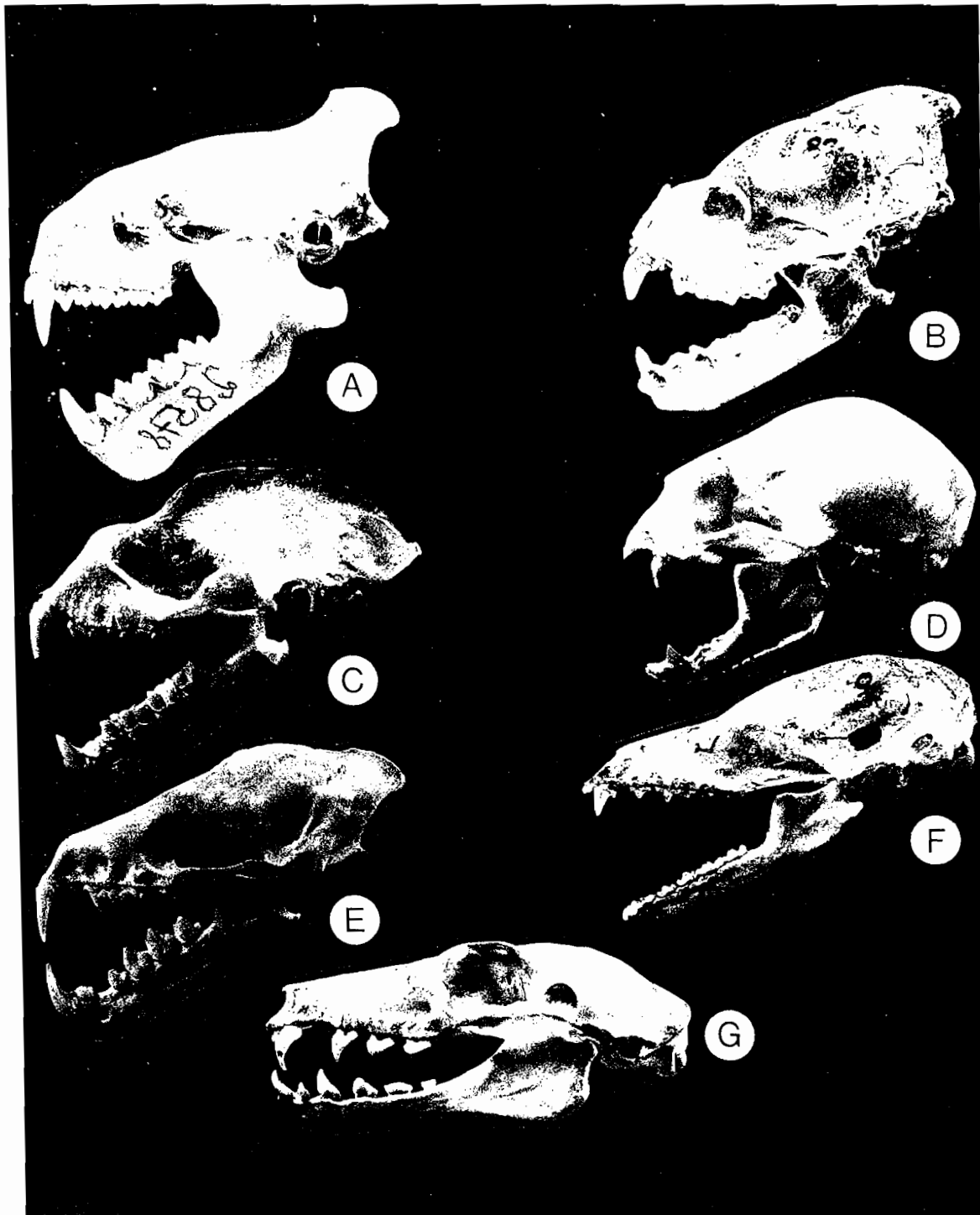
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Fig. 2.16 *Lateral views of cranium and lower jaw showing variation in cranial shape and sagittal crests.* A. Cheiromeles torquatus *(Molossidae)*; B. Taphozous saccolaimus *(Emballonuridae)*; C. Hipposideros diadema *(Hipposideridae)*; D. Diaemus youngi *(Phyllostomidae)*; E. Vampyrum spectrum *(Phyllostomidae)*; F. Leptonycteris curasoae *Phyllostomidae*; G. Epomophorus anurus *(Pteropodidae)*.

and 2.17D). In these bats, the nose is almost flat and the toothrows are curved into a flattened arch. A similar but less extreme tendency to shorten the rostrum is also found among genera of the microchiropteran family Vespertilionidae. The molossid *Tadarida gallagheri* from Zaire has greatly inflated rostral swellings similar to those of emballonurids, while in the Mouse-tailed bats (Rhinopomatidae) and the Old World leaf-nosed bats (Hipposideridae) the rostrum is swollen, or broadened and sometimes slightly raised by the inflation of its interior compartments. In the Horseshoe bats (Rhinolophidae) the anterior part of the rostrum is inflated dorsally by paired swellings that merge to form a distinctly dome-like structure. Rostral swellings such as these may be connected with the emission of the high frequency sounds used by these bats in acoustic orientation (echolocation).

The form and structure of the premaxillary bones varies more in bats than in any other group of vertebrates except, perhaps, some bony fishes and snakes. The reasons for this variation are not fully understood. The paired premaxillary bones carry the upper incisors and typically they are fused to the maxillary and palatal bones by vertical nasomaxillary and horizontal palatal branches, respectively. In addition, the two members of the pair may be fused together at the midline. The typical condition is found among noctilionid, mormoopid, phyllostomid, and molossid bats. In three families (Rhinopomati-

dae, Craseonycteridae, and Emballonuridae), the palatal branches of the premaxillary bones are greatly reduced. The denticulous nasomaxillary branches of the premaxillaries articulate (not fused) in a groove on the front of the maxillary bone. The members of the pair may be independent and unfused (Emballonuridae), fused on the midline below the nasal aperture (Rhinopomatidae), or fused above and below the nasal aperture (Craseonycteridae). A condition similar to that found in the Emballonuridae exists in the Megadermatidae, but the nasomaxillary branch of the premaxillary is extremely reduced (thread-like) and all incisors are absent. These tiny bones are frequently lost when the cranium is prepared for study and this has led some bat biologists to conclude wrongly that they are absent in this family. In the Rhinolophidae and Hipposideridae, the nasomaxillary branches are absent and all that remains of the premaxillary bones are the paired palatal branches that jut forward between the large canine teeth. These bones are fused together but their fusion to the palatal bone is rather weak and they may be flexed upward. A similar arrangement is encountered in the Nycteridae, although these bones are somewhat larger in size in this family. In the remaining vespertilionoid families, the palatal branches are lost and the nasomaxillary portions of the premaxillary bones are solidly fused with the maxillary bones. In addition, the two members of the pair of premaxillaries are widely separated (unfused) at the midline. This
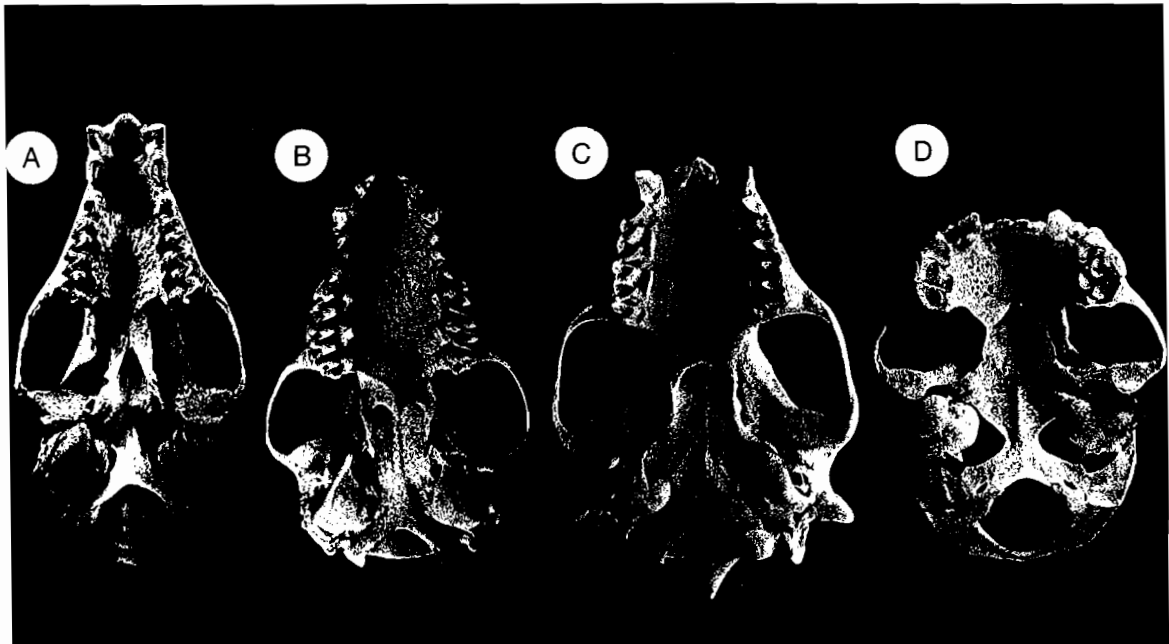

Fig. 2.17 Palatal view showing modification of nose and toothrows. A, Micronycteris hirsuta *(Phyllostomidae); B*, Pizonyx vivesi *(Vespertilionidae); C*, Cheiromeles torquatus *(Molossidae); D*, Centurio senex *(Phyllostomidae).*

results in a deep U-shaped cleft at the front of the cranium (Fig. 2.17B).

The post-cranial axial skeleton of bats reflects modifications more typically associated with flight. The bodies of bats are relatively short (Fig. 2.14). This is expressed in the antero-posterior compression of the individual vertebrae of the vertebral column. Not only are the vertebrae compressed, but their articular surfaces fit snugly together thereby greatly restricting their individual movement. In some families (Nycteridae, Rhinolophidae, Hipposideridae, Megadermatidae, Molossidae, and some species of the Vespertilionidae), the last cervical (neck) vertebra is fused solidly to the first thoracic vertebra. In the Hipposideridae, this fusion incorporates the second thoracic vertebra as well. The first and second thoracic vertebrae are fused in the Thyropteridae. In several other families there is extensive fusion of the lumbar (lower back) vertebrae. These include the Craseonycteridae, Hipposideridae (part), Mormoopidae (part), Natalidae, and Furipteridae. The sacral (hip) vertebrae are also fused for the most part. These fusions in the axial skeleton promote the rigidity and limited movement of the main body axis which facilitates flight.

The rib cage and sternum are other portions of the axial skeleton. The rib cages of bats are proportionately larger than those of other mammals of comparable size. In addition, they are considerably broader and deeper than those of other mammals (Fig. 2.14). The ribs themselves are markedly broadened and those in the anterior portion of the rib cage nearly touch. In hipposiderids, there is considerable fusion in this region.

The sternum (breastbone) is T-shaped in most bats (Fig. 2.14). The manubrium (anterior element of the sternum) is greatly enlarged. In hipposiderids the manubrium is fused with a number of the ribs and the entire complex is shield-shaped or plate-like. Often there is a short keel-like flange on the manubrium. The remaining sternal elements are usually fused into a single flat bar. The expanse and degree of fusion of the rib cage and the sternum all contribute to providing a solid surface on which the enlarged flight muscles attach.

The scapula (shoulder blade) is an important component in the wing skeleton of bats. In birds, this bone is long and narrow. In most mammals, the scapula is triangular or subtriangular in shape. It is roughly rectangular in bats, presumably to accommodate the attachment of the flight muscles (Fig. 2.14). The scapula is anchored to the massive sternal complex by the long and slightly bowed clavicle (collar bone).

Above we commented on the unusual modifications of the hindlimb. The rotation of the femur is also reflected in the shape of the pelvic bone. The ilium or innominate bone is rotated so that the gluteal surfaces (attachment sites for the gluteus muscles) are directed upward rather than to the side as in terrestrial mammals. The acetabulum (articular socket for the femur) also faces dorso-laterally.

Muscular system

Of all the internal systems of vertebrates, the muscular system is perhaps the most adaptable. Thus, while bats have a mammalian muscular system, there are many marked differences between the muscle arrangements found in bats and those of terrestrial mammals. These differences involve the relative sizes of muscles as well as their attachments and functions. In terrestrial mammals, the limbs are postured beneath the body and are nearly vertical to the ground. The modes of locomotion used by terrestrial mammals are varied, but most rely on an antero-posterior movement of the limb. This movement requires the interaction of muscles that move the limb back and forth. In bats, the wings stretch out to the sides of the body and move in an up-and-down manner. This requires the interaction of a somewhat different set of muscles than are used by terrestrial mammals. In addition, bats possess five muscles that do not occur in any other mammals. These all extend into and are involved with controlling the flight membranes. They are: M. occipito-pollicalis, M. coraco-cutaneus, M. humeropatagialis, M. plagiopatagii, and M. depressor ossis styliformis. The latter muscle is rigged between the calcar and the ankle and facilitates the spreading of the uropatagium. These and other flight muscles will be considered in more detail in Chapter 4.

The muscles that are not involved in flight are essentially similar to those of other terrestrial mammals. These include the jaw and head musculature which as noted above is influenced by the dietary habits of bats.

Nervous system

The nervous system of bats has not been studied extensively. Nonetheless, the structure and organization of this system seem to reflect modifications relating to flight adaptations and those involved with orientation in the environment. The apparent differences between the two suborders of bats (Mega- and Microchiroptera) have been the focus of most of the studies to date. As is the case with many other aspects

of chiropteran form and structure, the nervous system exhibits both primitive and specialized features.

The nervous system of bats and other vertebrates may be divided into two functional units. These are the central nervous system (brain and spinal cord) and the peripheral nervous system (ganglia and nerves). Very little is known about the peripheral nervous system.

The brain of bats is variable in size and this seems to be closely associated with body size. Other variations in the brain relate to differences in diet, locomotion, and mode of orientation. The brain may be divided into two basic parts: the forebrain (cerebrum or neocortex); and the hindbrain (cerebellum and medulla oblongata or brain stem). Generally speaking, the forebrain is much enlarged in the Megachiroptera, whereas the hindbrain is well developed in the Microchiroptera (Fig 2.18). The phyllostomids (Microchiroptera) have a rather large forebrain and are, therefore, somewhat exceptional in this regard. The forebrain consists of the olfactory lobes and the neocortex. Mammals, as a group, are distin-guished from all other vertebrates by having a well-developed neocortical region. The neocortex is enlarged to accommodate the location of many nerve centres that are either absent or were formerly located in the hindbrain of other vertebrates. One of the nerve centres that is found in the neocortex is that associated with vision. This seems to account for the large neocortical regions found in megachiropterans which rely heavily on visual orientation rather than acoustic orientation (echolocation) as used by micro-chiropterans. Phyllostomids also have large eyes as well as a well-developed sense of smell (olfaction) the nerve centres of which are also located in the neocortex. The enlargement of the neocortex is generally regarded as a specialized condition and, indeed, higher Primates (including man) also have large cerebral hemispheres. Microchiropterans have a neocortical region, but it is less well developed and in these bats the hindbrain is rather large. The nerve centres associated with acoustic orientation are found in this region of the brain. Also, most of the motor control centres for flight are housed here. In many
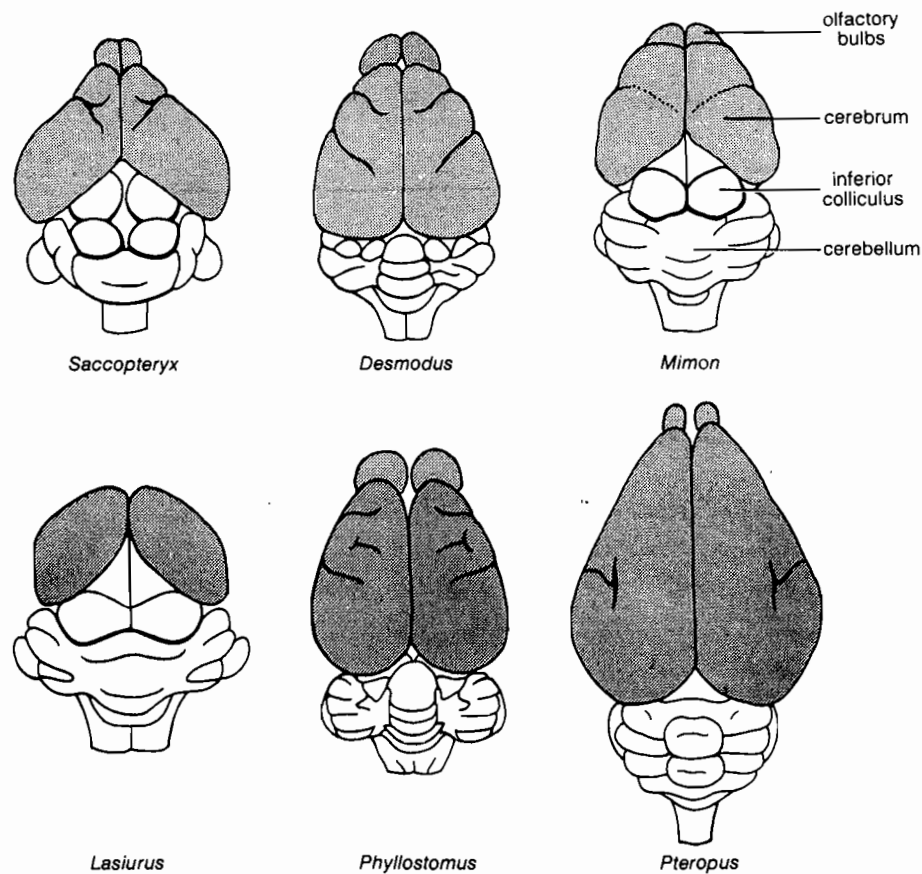

Fig. 2.18 Diagrammatic view of the brain in Saccopteryx (*Emballonuridae*), Desmodus, Mimon (*both Phyllostomidae*), Lasiurus (*Vespertilionidae*), Phyllostomus (*Phyllostomidae*) and Pteropus (*Pteropodidae*).

microchiropterans (except phyllostomids), the olfactory lobes are very small. We shall discuss additional aspects of the brain in Chapter 8.

The spinal cord of bats is greatly shortened; that of microchiropterans is perhaps the shortest known among mammals. In *Pteronotus parnellii* (Mormoopidae), the spinal cord ends at the level of the twelfth thoracic vertebra and in *Artibeus jamaicensis* (Phyllostomidae) at the eighth or ninth thoracic vertebra. This is roughly equal to approximately half the length of the human spinal cord. The general reduction of the locomotory function of the hindlimbs seems to account for this marked truncation in the spinal cord of bats. In humans and other mammals there is an enlarged swelling in the upper portion of the spinal cord called the cervical enlargement. Many ganglia and nerves associated with the movement and control of the arm enter and leave the spinal cord at this swelling. In bats, the cervical enlargement begins just behind the brain and extends for nearly half the length of the shortened spinal cord. This, of course, reflects the influence of having wings and flight. There are also some interesting differences in the spinal cords of mega- and microchiropterans. Lying along each side of the spinal cord are a series of ganglia that receive peripheral nerves and shunt these by way of the dorsal root into the spinal cord. Nerve impulses travelling along these nerves enter the grey matter of the spinal cord where their information is transmitted to the brain and back out to the peripheral regions as an action response via the ventral root. The entry and exit of dorsal and ventral roots, respectively, differs between the two suborders. A large mass of white matter (dorsal funiculus) wedges into the top portion of the spinal cord in megachiropterans and other mammals. As a result the dorsal root enters the spinal cord in a dorso-lateral location (Fig. 2.19). The dorsal funiculus is deeply embedded in the spinal cord of microchiropterans and the dorsal root enters at the dorsal midline of the cord (Fig. 2.19). This latter condition is unique among mammals and therefore appears to be a specialized adaptation of microchiropterans. The functional ramifications of these two distinctive types of spinal cord are not known.

Circulatory system

Compared to the extremely diverse evolutionary radiation in the chiropteran body form, the known modifications in the circulatory system seem to have been rather conservative. Most of the changes relate to functional requirements associated with flight or concern thermoregulatory adaptations reflecting the development of daily torpor and hibernation in some
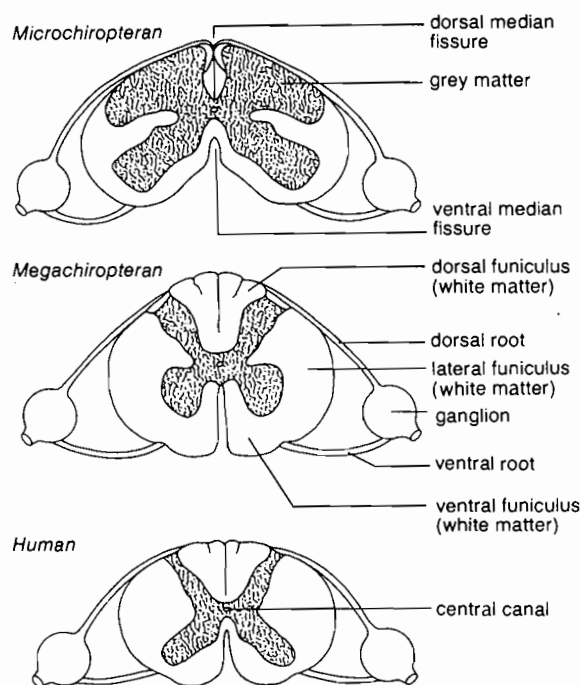

Fig. 2.19 Diagrammatic cross-sectional views of the spinal cord of bats compared to that of a human. See text for discussion.

species. These specializations will be discussed in Chapters 4 and 6.

The most prominent organ of the circulatory system is the heart. Bat hearts are extremely large relative to their body size. The heart of the European mouse-eared bat (*Myotis myotis*–20 g) is nearly three times larger than that of a laboratory mouse of equal weight. As a direct result of body shortening, the position of the heart in bats has been modified. In the generally long-bodied megachiropterans the heart is located near the centre of the chest and only slightly tilted to the left. However, in the short-bodied microchiropterans, the heart is rotated and assumes a nearly transverse (sideways) position. Overall, the hearts of bats tend to be more elongated than in other mammals.

Heart rates (beats per minute) are strikingly higher in bats than in most other mammals. However, there is considerable variation depending on the environmental temperature and the state of activity of the individual. The heart rate of active (flying) pteropodids at a thermoneutral temperature (approx. 30°C) ranges between approximately 100-400 beats min^{-1}. In microchiropterans, heart rates as high as 900-1000 beats min^{-1} (*Eptesicus fuscus*) are frequently recorded. During daily torpor, heart rates in microchiropterans drop to 40-80 beats min^{-1}, whereas in hibernating

individuals, heart rates as low as 20 beats min^{-1} have been reported.

In addition to large hearts and high heart rates, bats have correspondingly impressive stroke volumes (the amount of blood pumped by the heart in one beat cycle). The right ventricle is large in size and this appears to be directly related to the large quantities of blood pumped during any single stroke. Furthermore, the internal structure of the heart, primarily the arrangement and muscularity of anti-backflow valves, correlates with these increased stroke volumes.

The coronary circulation (the heart's blood supply) is much larger and more expansive in bats than in other mammals. Likewise, the pulmonary (lung) circulation is greatly enhanced compared with that of other mammals. These features of bats make them good medical research models for understanding human pulmonary and cardiovascular problems.

Other than special modifications of the arteries, veins, and capillaries in the flight membranes, the peripheral circulation of bats does not appear to be much different from that found in other mammals. There are fewer, but larger, vessels in the shoulder region of bats than are found in other mammals.

Bats have the unique ability to control (regulate) the quantity of blood circulating in the wing at any particular time. This control of blood dispersal and movement in the extensive capillary network of the wings is accomplished with special shunts or valves. Depending on the circumstances, the circulation of blood in whole segments of the wing may be cut off or greatly reduced. This ability is especially important since the wing membranes are excellent heat exchangers and the controlled reduction or increase of heat loss provides an efficient means of regulating the internal body temperature of these warm-blooded animals. For example, during flight, a considerable amount of excess heat is generated and this is dissipated (radiated) across the flight membranes by opening the capillary shunts. On the other hand, these are closed to conserve heat while the bat is at rest.

Digestive system

In general organization, the digestive system of bats is essentially like that of other mammals. However, the wide variety of food habits found among bats is reflected in the anatomy of some components of this system, especially the stomach and intestine. The digestive system of bats has not been well-studied, but a fair amount of information exists for the New World leaf-nosed bats (Phyllostomidae). This micro-

chiropteran family also exhibits the widest range of food habits, including nearly all of those found in bats. A more detailed discussion of the digestive system will be presented in Chapter 5.

Urinary system

Relatively little is known with regard to the urinary system of bats. This system includes the kidneys, ureters, urinary bladder, and urethra. Its primary function is to maintain a physiological balance (homeostasis) between water and salt (various electrolytes) concentrations in the body. In other mammals, the urinary system (primarily the kidneys) responds (is adapted) to different diets (watery or salty) and/or differences in habitat, especially arid or semi-arid regions where free-standing, fresh drinking water is at a premium. The mammalian kidney is highly specialized for water conservation compared to those of other vertebrates and it produces a high concentration of urea in the urine.

There is little to indicate that the kidneys of bats are markedly different from the generalized mammalian kidney. As noted above, the bodies of bats are generally shortened and we noted that the position of the heart was altered by this modification in body proportion. The kidneys are located somewhat lower in the abdomen of bats than in other mammals and the right kidney may be positioned slightly higher than the left. The right kidney may even be embedded in a dimple in the right lateral lobe of the liver.

Bats occupy a number of different and diverse habitats (see Chapter 9) and, as a result, face a variety of water/salt balance situations. For example, after a blood meal, vampire bats face three important water problems. The first two are physiological and, initially, concern excretion of the excess water in the blood meal which would overly dilute the concentration of body fluids. Later, the digestion of the high protein content of the meal requires the conservation of water. The third concern is aerodynamic and also requires the excretion of excess water in order to lighten the overall weight of the bat so that it can fly. Fruit-eating species also need to dispose of excess water. The protein content of their foods is not as high as that of blood and, since most inhabit tropical regions of the world where free-standing drinking water is usually available, water conservation is not so much of a problem.

Another interesting physiological problem is found in the Fishing bat (*Pizonyx vivesi*) that lives in the arid regions of Baja California. These bats often forage over marine lagoons and eat marine fish that are generally high in salt content. In addition to this,

these bats also face the normal problems of desert environments; that is, water conservation. Like many other desert-dwelling mammals, the kidneys of *Pizonyx* are specially adapted to conserve water and excrete a highly concentrated urine. These bats may even drink seawater which would fatally tax the kidneys of normal mammals.

Bats that hibernate also face a water conservation problem. This is alleviated somewhat by selecting hibernation sites that have a high relative humidity, thus reducing loss of water by evaporation. Also, metabolic water is released into the system as the fat stores are broken down during this period of lower metabolic activity (see Chapter 6). The kidneys of these bats are adapted to conserve and use metabolic water during this period of inactivity. Some hibernating bats such as the Western pipistrelle (*Pipistrellus hesperus*), which inhabits the southwestern deserts of the United States, frequently awaken during intermittent warm spells and drink water to replenish their depleted reserves. During these periods of arousal, they may also feed on any insects that happen to be out.

Reproductive system

The wide diversity of reproductive patterns found among bats (see Chapter 7) contrasts with the anatomical aspects of their reproductive systems that are basically the same as those in other eutherian mammals. There are, however, a few noteworthy specializations that might be mentioned here.

The ovaries and ovulatory processes in bats are essentially like those of other mammals. The ovaries of hibernating bats with delayed ovulation develop special glandular tissue around the mature ovum and maintain it through the hibernation period. Ovulation and fertilization in these bats occur early in the spring at the time of emergence or shortly before. In others, ovulation and fertilization occur prior to entering hibernation and the unimplanted embryo is maintained in a quiescent state through hibernation. In still others, copulation occurs prior to or during hibernation and the uterine mucosa is specially adapted to maintaining the live sperm throughout the hibernation period.

Like most mammals, nearly all bats ovulate from either ovary; that is, ovulation is symmetrical. In some bat species, ovulation is restricted to either the right or left ovary. Right-sided ovulators include members of the Vespertilionidae, Natalidae, Rhinolophidae, Hipposideridae, and Mormoopidae. Left-sided ovulators include members of the Molossidae and Megadermatidae.

In all mammals, the ovaries produce specific hormones (estrogens and progesterones) that travel in the blood to the uterus where they cause specific physiological and morphological responses. In the few bats that have been examined, there is a special set of blood vessels that runs between the ovaries and uterus and facilitates the transport of these hormones.

The uterus of bats is generally bicornuate; that is, there is a single and distinct uterine body which divides into two uterine horns. In all of the New World leaf-nosed bats (Phyllostomidae), except *Macrotus*, *Micronycteris*, and the vampires (Desmodontinae), the uterine horns are completely fused to form a single or simplex uterine body. A similar uterus is found in higher Primates such as man. The asymmetry mentioned with regard to the ovaries is also found in the functional development of right and left uterine horns. Typically, in eutherian mammals, fertilization occurs in the oviduct and the blastocyst (zygote or embryo) migrates to the uterus where it implants and undergoes its gestational development. There are generally no specializations in the oviducts. In bats, the walls of the oviduct, in which fertilization occurs, become highly glandular and the blastocyst may pass some time therein before moving to the uterus and subsequent implantation. Implantation sites are variable among bats, but are usually near the oviduct/uterine junction.

The mammary glands of bats are paired and located in the pectoral region as in Primates. However, their position is more axial (nearer the armpit) than in Primates. The location of the mammae in this region may relate to aerodynamic considerations involving placement of the centre of gravity when the female is carrying nursing young. Several families (Rhinopomatidae, Craseonycteridae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae, and some species of the Vespertilionidae) have an additional pair of teats located in the inguinal region (near the groin) just above the external genitalia. These do not secrete milk, but serve as a holdfast for the young bat while the mother is in flight.

The male reproductive tract of bats is less specialized than that of the female. The testes may be seasonally active or active year-round. They may descend into a discrete scrotum or they may be maintained in an abdominal pouch. In vespertilionids, the testes descend into a scrotal sac that has been incorporated into the uropatagium on either side of the tail. The penis, which becomes erect through vascular engorgement is pendulous in most bats and similar in appearance to that of Primates. It varies considerably in size and structure, reaching an extreme in *Scotoecus* where its length may approach that of the upper leg bone. Among other vespertilionids the penis of Hemprich's Long-eared bat

(*Otonycteris hemprichi*) has a curious appearance, the glans (head) expanded vertically to project between two lateral swellings, with a third dorsal swelling above and behind it, while in the New Guinea Brown bat (*Philetor brachypterus*), the penis is similarly complex, the glans emerging from a swollen preputial structure that dorsally bears a small cushion-like pad covered with short, stiff bristles and projects ventrally as a preputial flap or fold. In some species, again especially in the Vespertilionidae, the prepuce may contain erectile tissue that facilitates copulation in these bats. Many bat species have a reduced os penis or baculum (penile bone); its form may be simple or complex.

Chapter 4 *Flight*

Bats are unique among mammals in their possession of wings and their ability to move about under true sustained flight. Unlike birds, which can simply fold their wings when not in use and walk about on relatively unspecialized hindlimbs, bats are essentially incapable of alternative forms of locomotion when not in flight. Of course, all bats can scurry about to some extent and vampires (Desmodontinae) are quite agile, walking on their elbows and wrists. However, by virtue of their anatomical adaptations for flight, bats have largely abandoned their terrestrial (i.e., quadrupedal) locomotory abilities. No other volant animal, except the reptilian pterosaur, has made such a drastic and complete modification in its locomotory style.

Among vertebrates, the ability to achieve true sustained flight must be considered a rare event having occurred only in birds and bats. Pterosaurs (prehistoric reptiles that became extinct at the end of the Mesozoic Era, about eighty million years ago), possessed wings that in some respects resembled those of bats. Indeed, some of the smaller species of pterosaurs may have been capable of flapping flight, although most probably used their wings to soar. Insects (invertebrates) are the only other group of animals to possess the capability of sustained flight.

The rarity of adaptations for true flight, among vertebrates at least, appears to be associated with a wide array of morphological, physiological, and aerodynamic factors that preclude aerial locomotion by most vertebrates. However, once developed, flight confers a distinct evolutionary advantage to those organisms that possess it. The capture and exploitation of flying insects as a food source (aerial insectivory) is absolutely restricted to flying birds and bats. In microchiropteran bats, the development of acoustic orientation (echolocation) has allowed them to carry this unique foraging strategy into the nocturnal realm. Other benefits accrued from flight include: escape from predators; expanded daily foraging ability; potential for dispersal across barriers that are otherwise insurmountable, or nearly so, by non-flying, terrestrial animals; long-distance, seasonal migration; and occupation of roosting and nesting sites not readily available to non-flying animals. To say that flight was the sole factor accounting for the

diversification and radiation of birds and bats would be much too simplistic. Nonetheless, flight apparently has been a primary contributing factor in the evolution and success of these groups.

Regarding pterosaurs, the evolutionary innovation of wings in this group of reptiles certainly must have conveyed some of the benefits noted above. However, the known diversity of this group (20 genera) does not approach that of either birds or bats and, indeed, the lack of further refinements of the wing for sustained flight may have contributed to the demise (extinction) of these 'flying' reptiles. Competition with birds is often cited as the cause for the extinction of pterosaurs. This seems unlikely and we suspect that the failure of pterosaurs concerns more the inadequate design and structure of their wing and its limited use as an efficient flying device.

There can be little doubt that the possession of wings and flight were important in the evolution and adaptations of insects. But, the loss or absence of wings in many species and/or life stages of species (larvae, pupae, etc.) as well as an array of other modes of locomotion, would seem to suggest a role of lesser importance for flight in insects than in flying vertebrates.

The importance of aerial locomotory adaptations is further illustrated by the number of vertebrates that have acquired the ability to glide. Gliding usually results in the loss of altitude over a given distance, is never sustained, and, therefore, cannot be categorized as true flight. On the other hand, adaptations for gliding are much less drastic, in terms of anatomical modifications, and less rigorous, in terms of aerodynamic constraints. Gliding, among non-mammalian vertebrates, occurs in 'flying' fish, several 'flying' frogs (*Rhacophorus* and some hylids), several 'flying' lizards (*Draco*–Agamidae and *Ptychozoon*–Gekkonidae), and a 'flying' snake (*Chrysopelea*–Colubridae). In flying fish, the pectoral fins are enlarged, and various sorts of webbing between the toes and lateral abdominal flaps of skin are utilized by flying frogs and the flying gekko. *Draco* and the flying snake utilize special, extendible ribs and associated membranes in their gliding adaptations.

Gliding adaptations occur in several groups of mammals and include: Sugar gliders (Order Marsu-

pialia); the 'Flying' lemur or Colugo (Order Dermoptera); and several different groups of 'Flying' squirrels (Order Rodentia). All have an elastic membrane along the sides of the body joining the legs. The fingers and toes of the Sugar gliders and all Flying squirrels are not webbed and there is little or no membrane in front of the forelimb or between the hindlimbs. The tail remains free, for the most part, and it is usually quite bushy, except in Scaly-tailed flying squirrels. Colugos have more extensive membranes including: webbing between the digits of both the hand and foot; between the forelimb and neck (propatagium); and between the hindlimbs including the tail (uropatagium). Like most bats, Colugos have difficulty locomoting when on the ground, but, in the air, they are quite graceful and capable of gliding flights of several hundred metres. The general resemblance of the rigging of the flight membranes of Colugos to that of bats has prompted the notion that bats evolved through a 'colugo-stage' in their evolution. Unlike Colugos, the toes of the foot are not webbed in bats and the thumb is largely free. During gliding sorties, Colugos move their hands in an up-and-down fashion, not flapping as in bats, but they are able to effect various turns and other altitudinal manoeuvers. While Colugos are not the ancestors of bats, they do appear to be closely related to bats, especially to the Megachiroptera.

ANATOMICAL REQUIREMENTS FOR FLIGHT

True sustained flight requires three basic anatomical modifications for versatility and efficiency. First and foremost is the development of a wing of sufficient length and with specific aerodynamic characteristics that will allow it to lift and support the body and associated payloads (e.g., food or prey items; reproductive products such as developing embryos or suckling young, etc.) during flight activity. Secondly, sustained flight requires a source or means of propulsion, and thirdly, the body must be sufficiently streamlined to permit efficient flight that is both aerodynamically feasible and metabolically economical.

The events leading to an historic winter morning (December 17, 1903) at Kill Devil Hills, near Kitty Hawk, North Carolina, when man first achieved true sustained flight, are an interesting history of the human experience and the development of powered flight. A wealth of mythological writings and drawings portray man's early dreams of flight. Most of our first experiments with flight involved attempts to emulate the flapping flight of birds with various

bird-like wings and contraptions. Some early, would-be aviators even covered their bodies with feathers in the hope that these would provide the essence of flight. The successful pathfinders settled on fixed-wing devices and experimented with gliding and soaring. The next task was to find a sufficient, non-flapping means of powering their winged aircraft. This, of course, led to various propeller-like contraptions and eventually to the successes at Kitty Hawk. Man's breakthrough with flight is no less an evolutionary event than the development of flight by animals. Note the rapid radiation and diversification of aircraft in the past eighty years and the marked influence of these on the social and technological aspects of human culture.

Although man took many cues from flying animals, especially birds, in his development of powered flight, he has not been able to equal the dynamics and manoeuverability of flapping flight. In all truly flying animals, including insects, the wing serves a dual function. It provides the aerodynamic lifting qualities required for flight as well as the driving, propulsive force for sustained, powered flight. The wings and general appearance of pterosaurs, bats, and birds are similar. However, each of these animals has developed these structures in drastically different anatomical ways and the flight characteristics of these respective groups are markedly different.

Pterosaur wing

Like birds and bats, the wing of pterosaurs evolved through the modification of the forelimb. Proceeding outward from the shoulder joint, the proximal portion of the pterosaur wing consisted of the humerus and the fused radio-ulna (Fig. 4.1A). Next came the compacted carpals of the wrist, and then the elongated metacarpals of four digits (2-5), closely bound together. At this level of the wing, three fingers (2-4) were more or less normal in appearance, free of the wing proper, and directed forward, these presumably were used to grasp and climb about. Beyond this level of the wing were four elongated phalanges of the fifth finger. [There is some confusion regarding the loss of the thumb (digit 1) or the fifth finger. Some authors identify the long finger of the pterosaur as the fourth digit thereby implying the loss of the fifth finger. Others identify the four existing fingers as we have (2-5) and imply the loss of the thumb. On the anterior portion of the wrist region, there is an elongated and recurved bone (pteroid) that supports a propatagial flight membrane. It is difficult to determine, with certainty, whether or not this is a modified thumb or an osteological innovation. Without evidence to the contrary, we regard it as the thumb.] Like the bones of
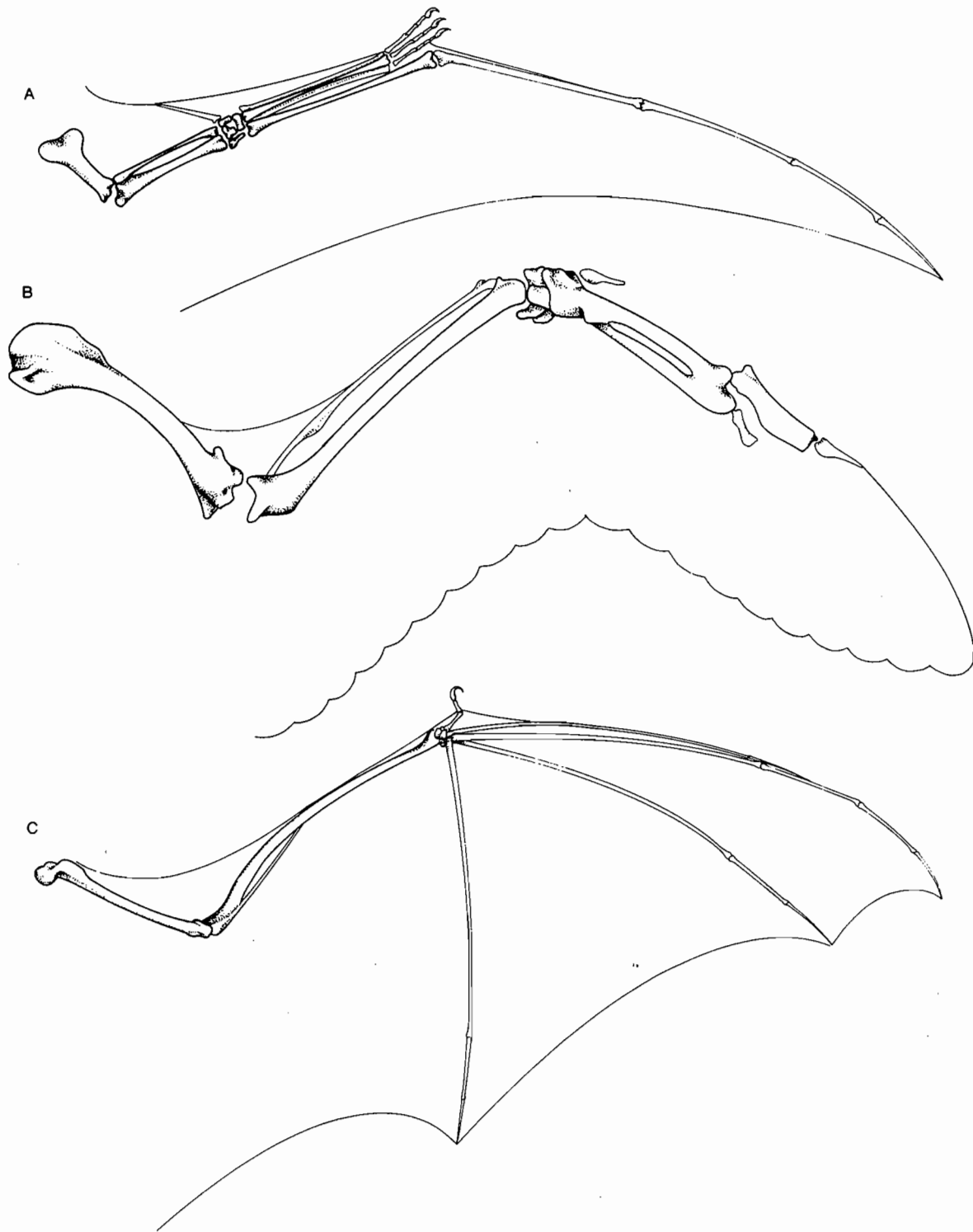
A

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C

Fig. 4.1 A, Wing of pterosaur; B, wing of bird; C, wing of bat.

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birds, the bones of pterosaurs were extremely lightweight and hollow or pneumatic (air-filled). The bones of bats are not pneumatic but those of the wing skeleton are very slender which contributes to low weight.

The main flight membrane was attached on the rear margin of the long wing spar that consisted of the arm and elongated fifth finger as described above. This membrane attached along the sides of the body and the elongated hindlimb. Such an arrangement surely would have hampered the mobility of pterosaurs on the ground. As noted above there was a propatagium attached to the pteroid (thumb?) bone. The control of this flight membrane was accomplished by a pteroid muscle that attached to the anterior margin of the humerus.

The wing of pterosaurs was similar to that of bats in that it was an elastic, membranous wing as opposed to a feathered wing as found in birds. The control of wing camber (see below) would have been extremely limited in the pterosaur wing. Flexion of the body axis could have produced varying degrees of curvature. Presumably, there was a muscle, an elastic tendon, or a combination of these that extended from the tip of the fifth digit, along the rear edge of the wing, to the leg region. Such a device would have permitted the control, by tension, of the trailing edge of the flight membrane thereby causing different degrees of cross-sectional curvature of the wing. The wing of pterosaurs had reduced adaptive potential, mostly relating to the limited control of camber. Other aspects of pterosaur anatomy leave considerable room to doubt that their wings were capable of vigorous flapping movement as characterized by birds and bats. Gliding or dynamic soaring was probably the extent of their flight ability. As we noted earlier, this inadequate aerodynamic design may have been an important factor in their extinction.

Bird wing

The wing of birds is perhaps the most radical and novel structure ever to develop in the evolutionary history of vertebrates. Whereas the wings of pterosaurs and bats may also appear to be rather bizarre structures, they are rather simplistic in their modification of pre-existing structures. The proximal portion of the wing of birds consists of an elongated humerus, followed by separate, well-developed ulna and radius. Beyond these relatively unmodified bony elements, there is a drastic reduction and fusion of bony structures (Fig. 4.1B). Articulating with the radius and ulna is a large carpo-metacarpal bone (composed of fused carpals and metacarpals). The reduced first digit (thumb) articulates on the anterior,

proximal margin of this fused bone. Distally, the much shortened phalanges of the second digit and the vestigial remains of the third digit attach to the carpo-metacarpal.

The main portions of the wing (flight surfaces) are made up of several different kinds of feathers (themselves unique and complex structures) that attach to the rear portion of the main spar of the wing described above. Long, stiff primary feathers attach to the carpometacarpal and phalanges of the second digit. Specialized, primary-like feathers attach to the thumb or first digit; it is usually referred to as the alula. Somewhat shorter, but stiff secondary feathers attach to the ulna. The contour of the upper side of the wing is provided by a series of specialized feathers known as lesser, medial, and secondary coverts. The contour of the underside of the wing is provided by lesser under and greater under coverts. As should be apparent, the cross-sectional shape of the wings of birds is fixed much like that of wings of airplanes. Certainly, man has devised ways of changing the cross-sectional shape of his wings. The point to be made here is that unlike bats, and perhaps pterosaurs to a lesser extent, birds cannot greatly modify the curvature (camber) of their wings. Like pterosaurs and bats, birds also have a propatagial fold of skin in front of the wing, between the shoulder and wrist. A muscle (tensor patagii longus) similar to that found in bats (occipito-pollicalis) and pterosaurs (pteroideus) controls the curvature of this membrane. Changing the shape of this membrane is virtually the only means of wing camber modification in the wing of birds.

The evolution of wings and flight in birds is a much debated topic. Whereas pterosaurs and bats are presumed to have passed through a gliding stage that required a launch site from trees or heights above the ground, the development of bird flight is not so tied to such a progression. An outstanding feature of birds is that virtually all possess a dual locomotory system with wings for flight (some for swimming such as penguins) and hindlegs for normal bipedal walking and running. Indeed, birds are thought to have evolved from already bipedal, reptilian ancestors. Thus, birds could have evolved flight from either the ground or from arboreal situations; the former seems likely.

Bat wing

We have already described the general anatomical aspects of bat wings in Chapter 2. To summarize briefly, almost no part of the forelimb of bats has been reduced or lost. On the contrary, all elements, except those of the thumb, are greatly elongated and very

slender; the ulna has been reduced and in most species is restricted to the elbow region (Fig. 4.1C). The pelvis and hindlimbs are much less developed than in birds, and the legs are so totally involved in the support and control of the wing membranes that they have lost the normal quadrupedal ability of other terrestrial vertebrates. As noted earlier, many bats have a membrane (uropatagium) between the legs that often includes the tail or a portion thereof. This permits an increase in the total flight surface area.

PRINCIPLES OF AERODYNAMICS

In simple terms, flight depends on the overall effect of four forces—lift (upward force), drag (resistant rearward force), thrust (forward force), and gravity (downward force)—as air moves over and under the surface of the wing. As we have noted above, wings always have some degree of cross-sectional curvature; that is, they are not flat. Thus, a wing or airfoil may be characterized as being convexly curved on the upper side; the underside may be flattened or somewhat concave (Fig. 4.2). The degree of curvature

or convexity is referred to as camber and the extent to which this curvature can be modified is referred to as 'camberability.' Such cambered flight surfaces have a particular characteristic that permits flight to occur. As a stream of air strikes the leading edge of a horizontal airfoil, it is divided into two layers (Fig. 4.3A). One of these layers flows over the top surface of the airfoil while the other layer passes along the bottom surface of the airfoil; these two layers are reunited when they meet behind the trailing edge of the airfoil. Because of the convex curvature (camber) of the upper surfaces of airfoils, the air that flows over the top side of wings must move faster than the air passing under the relatively flat lower surface. As a result of the faster movement of air on the top side of airfoils, a negative pressure occurs (following Bernoulli's theorem). This negative pressure on the top side of the airfoil causes the wing to rise. The force resulting in this levitation is called lift. Two factors that effect lift in a positive way are: 1) the speed of the air as it flows over and under the airfoil or the speed that the airfoil moves through the air (this is called relative wind); and 2) the degree of convexity or camber of an airfoil. To a point, as these two factors
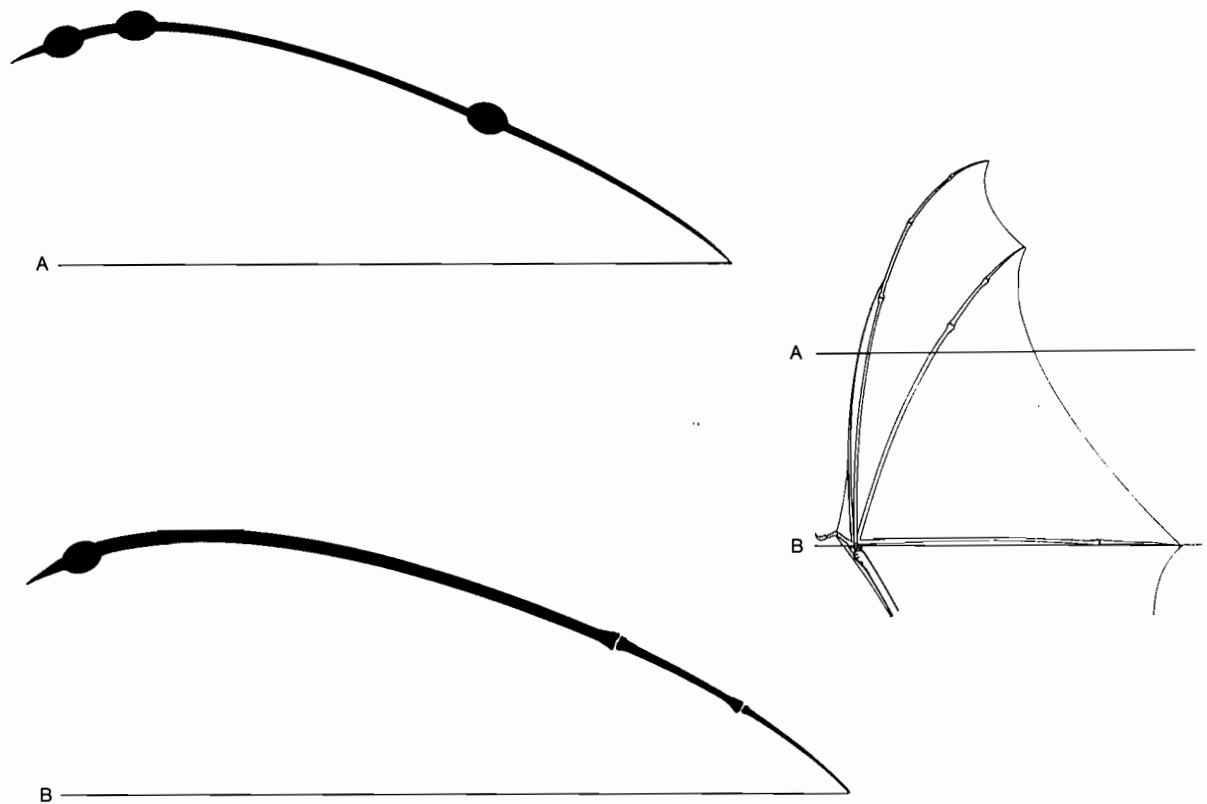

Fig. 4.2 Cross-sections (A, B) of the bat wing. The camber is produced by the supporting digits (After Norberg, 1972a and b).
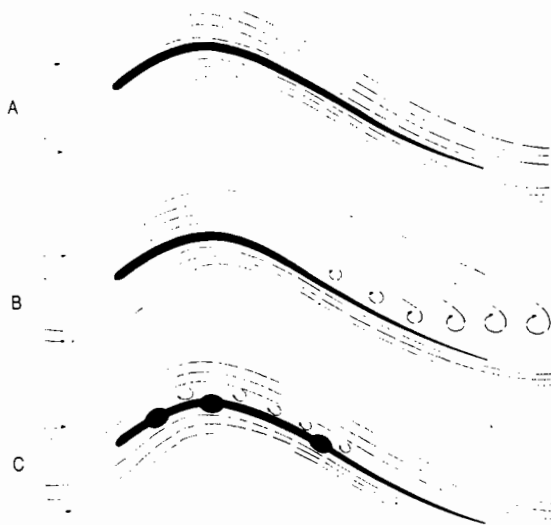
Fig. 4.3 A, Air flow above and below the wing; B, air flow with turbulence above rear of wing; C, the rounded projection of the digits helps to reduce turbulence and drag.

are increased, lift also increases. In fact, there is an inverse relationship (trade off) between these two factors; greater camber permits a particular amount of lift at lower speeds of the air stream.

Another way to effect lift positively without changing the camber or air speed is to change the angle of attack. For example, if we tilt upward, slightly, the previously horizontal airfoil, we have changed the angle of attack. This change, like an increase in camber, causes the air flowing over the top of the airfoil to move faster, thereby causing a greater negative pressure, and so, an increase in lift. However, as we continue to tilt the airfoil upwards (increase the angle of attack), the smooth, laminar flow of air over the wing begins to pull away from the rear portion of the airfoil, thus creating an area of disruptive turbulence. This turbulence erodes the force of lift and it is referred to as drag. Increasing the camber of a horizontal airfoil has the same effect.

Drag counteracts the forces of lift and thrust. Drag force on a wing at a particular angle of attack can be countered by an increase in the speed of the air over the wing or by reducing the wing camber or the angle of attack. If the force of drag is allowed to increase (either by continually increasing the angle of attack, slowing the air stream, increasing the camber of the airfoil, or some combination of these), the turbulence on the upper side of the wing will eventually erode the lifting force to a point where the airfoil will cease to rise. At this point, the wing stalls, the force of gravity takes over and the flying object will fall. Stalling depends on the angle of attack and airspeed.

Birds, bats, presumably pterosaurs, and man all utilize controlled stalling when they land.

The upper surfaces of animal wings are rarely smooth; even the apparently smoothly contoured wings of birds have small irregularities that cause some minor turbulence in the layer of air nearest the wing (boundary layer). The bones and knobbly joints of membranous wings, such as those of bats, also cause minor turbulence. This minor turbulence is beneficial in that it causes the boundary layer of air to be held firmly on the wing surface (Fig. 4.3B-C).

Thus far, we have considered the aerodynamic characteristics of airfoils with regard to camber, angle of attack, and air speed. In addition, the aerodynamic performance and load-carrying capacity of a wing are also determined by its effective area and shape. Wing shapes vary along a continuum from short and broad to long and narrow. These dimensions are expressed in terms of aspect ratio. Aspect ratio is derived by dividing the wing span by its average width or chord. Since the average chord may be impossible to determine, aspect ratios (A) are usually determined by the formula, $A = \text{span}^2/\text{area}$. Long, narrow wings have high aspect ratios, while short, broad wings are low in aspect ratio. Wing loading (WL) is the weight of the flyer distributed over the area of the flight surfaces or $WL = \text{total weight}/\text{wing area}$. Since small animals have more surface area in relation to their volume than do larger animals of identical proportions, small birds and bats have relatively low wing loading without having especially large wings. Wings that have a high aspect ratio tend to have high wing loading values, although this is not always the case. High aspect wings generally have high performance characteristics—fast flight, hovering ability, or dynamic soaring ability. Low aspect wings generally have lower loading and are capable of lifting greater weight, are efficient at low speeds, and are more versatile (manoeuverable) than high aspect wings. On the average, bats achieve slightly higher aspect ratios than do birds and wing loading in bats tends to be lower, overall, than in birds.

BAT FLIGHT

The wing of bats may be divided into three discrete areas; each has a particular aerodynamic function. The propatagium is that portion of the flight membrane in front of the wing between the shoulder and the wrist. Its leading edge is controlled (stiffened) by the occipito-pollicalis muscle. When this muscle contracts, the leading edge of the propatagium is stiffened and pulled downward, thereby increasing the convexity (camber) of the leading edge. The

plagiopatagium is the large portion of the wing that attaches behind the humerus and elongated radius and stretches between the body and hindlimb to the fifth finger. This portion of the wing is the lift-generating section and its camber is controlled by flexing the body axis and/or the fifth digit. The length of the respective elements of this finger (metacarpal, first and second phalanges) will determine the amount and degree to which the surface area may be cambered. The uropatagium serves to increase the effective lifting area of the wing and operates in conjunction with the plagiopatagium. Also, it may act as an airbrake or, as we noted earlier, a receptacle for catching insects.

The propelling or power-generating portion of the wing is the dactylopatagium. This is the distal section of the wing and it stretches between the second and fifth fingers. The camber of this section of the wing may be changed by flexing the digits. And again, the amount and degree to which this area may be cambered depends on the respective lengths of the metacarpals and phalangeal elements. The membranous areas of the wing are reinforced by many elastic fibres and muscular strands.

These same lift and propulsive areas are present in the wing of birds but as we noted above, the avian wing is less dynamic; that is, incapable of marked changes in camber. However, birds may vary their wing area, aspect ratio, and wing loading by drawing the wings closer to the body. Bats are less able to do this because the elastic and membranous nature of their wings necessitates the full extension of the flight surfaces.

Wing beat cycle of bats

In flight the downstroke (or powerstroke) begins with the wings raised well above the horizontal over the back and extended slightly back and behind the centre of gravity. From this position, the wings are fully extended, having just unfurled from their folded posture in the upstroke (or recovery stroke). As the downstroke proceeds, the wings sweep forward and sharply downward at a high angle of attack. The body axis is convexly curved upward thereby causing the hindlimbs, tail, and uropatagium (in those species that have one) to be bent downward. Midway through the downstroke the plagiopatagium is strongly curved convexly by the air pressure under the wing pushing up on the taut, elastic membrane and by the flexure of the fifth digit. Thus, at this point in the powerstroke, the large plagiopatagial portions of the wings and the strongly cambered body and uropatagium are generating maximum lift. These

lift-generating surfaces retain this posture throughout the remainder of the powerstroke.

During the powerstroke, the dactylopatagium goes through a number of dynamic changes. Since this region of the wings generates the propelling force, these surfaces must generate forward movement. The spinning propeller of an airplane is no less an airfoil than the fixed wings of the airplane that it carries forward. The notable difference is that a propeller blade is oriented vertically in the airstream, whereas the wing is horizontal. Lift produced on the upper surface of the wing causes upward movement, whereas the lift produced on the front surfaces of the vertically oriented propeller causes forward movement. The blades of some propellers are mechanically arranged so that they can rotate at their root (near the hub). This allows the pilot to change the 'pitch' or the angle of attack of the spinning propeller to suit whatever the particular thrust requirements might be. The dynamic changes in the thrust-generating portion of a bat's wing are similar to the pitch modifications of a propeller. Although the dactylopatagium is not a spinning device like an airplane's propeller, its lifting surfaces behave like one, and indeed, these surfaces rotate, not in a vertical plane, but in the horizontal.

An analogy, using the human hand, will help explain the posture (pitch) changes of a bat's 'hand' (dactylopatagium) during the powerstroke. We should note here that thrust is produced during both the powerstroke and the recovery stroke. Note first that the human hand may be rotated (in the horizontal plane) from a 'palm down' posture (pronated) to a 'palm up' posture (supinated). While a bat's hand is not as mobile as the human hand, it is capable of limited pronation and supination. At the start of the powerstroke, the hand, in the pronated position with the top surface tilted forward, is brought forward and down at a sharp angle. Lift generated in this posture will not cause the hand to rise, but instead, to be pulled forward and slightly upward. As the powerstroke continues, the air pressure under the hand (or dactylopatagium) will cause the membrane to billow upwards (enhancing its camber) and also will cause the tip and rear margin to be bent upward, thereby further increasing the angle of attack. To this point, forward lift (thrust) has to be generated on the top surface of the hand (or dactylopatagium).

At the bottom of the powerstroke, the hand is quickly supinated, turned so that the palm faces forward and is tilted slightly rearward. This quick rotation (supination) in a bat's wing is called the 'flick' phase because of its 'snappy', rapid occurrence. The flick phase initiates the beginning of the recovery stroke. Several things happen in the recovery stroke,

the most important being the return of the wing to the top of the powerstroke. This must be accomplished with the generation of minimal drag. To do this, large portions of the wing (plagiopatagium) are collapsed or furled and the wings are raised (partially folded) over the back.

At the instant that the hand (dactylopatagium) is flicked forward, two things occur. First, the plagiopatagium is collapsed. During the powerstroke, air has been compressed beneath the entire wing and especially under the plagiopatagium. The supination of the dactylopatagium (to initiate the flick) affects the entire wing and causes the plagiopatagium to supinate slightly. This changes the orientation of the compressed air under the wing from an upward pressure to a rearward pressure. When the plagiopatagium is collapsed, this air pressure is released and it jets rearward causing the bat to be thrust forward. In effect the release of this air pressure acts like a mini-jet engine. Second, as the wing-tip is flicked, it pushes against the compressed air mass that it has generated during the powerstroke. This changes the inertia of the wing-tip and starts it on its way through the recovery stroke. The dactylopatagium does not fully collapse in the recovery stroke; instead it slices at an angle, upward and rearward. Because the wing has been supinated, the palm becomes the top surface. As it is drawn upward and rearward a small amount of forward lift is generated on the palmar surface. In the wing beat cycle, the wing-tip tracks through a figure 8. Thus, as a result of the pronation of the dactylopatagium through the powerstroke and supination through the recovery stroke, the wing-tip is rotated horizontally. Using first the camber of the top side then the camber of the underside, thrust (forward lift) is generated. At the same time, the cambered plagiopatagium, body, and uropatagium are capturing upward lift.

Flight is rarely conducted as a straight and level activity into a uniform, head-on airstream. Thus, manoeuvers such as climbing, diving, and turning are needed and corrections are required to compensate for irregularities or changes in the direction of the airstream. Thus, flying objects must be able to control pitch (up and down rotation), roll (rotation around the longitudinal axis), and yaw (side to side rotation). Airplanes are equipped with various control surfaces (movable or winged airfoils): ailerons in the wings control roll or assist turning; horizontal stabilizers in the tail control pitch and assist climbing and diving; a vertical stabilizer in the tail controls yaw and assists in turning. Co-ordinated (lift efficient or drag-minimizing) manoeuvers are accomplished by the careful manipulation of these mechanical control surfaces by the trained pilot.

Most flying animals do not have the benefit of separate control surfaces to conduct their manoeuvers. These are accomplished by subtle changes in the wing beat cycle or by differentially moving the wings during the wing beat. Birds and bats do have horizontal stabilizers of sorts; the tail or uropatagium. Up and down movement of the tail or uropatagium permits control of pitch. The usually long tail of birds can be moved freely from side to side and thereby control yaw. To a lesser extent, bats can rotate the uropatagium and compensate for changes in yaw.

Take-off

All airplanes require a certain distance or runway length to take off. During the take-off roll, the forward lift from the engine-driven propellers or the thrust of jet or rocket engines pull or push, respectively, the wing(s) through the air until sufficient lift is generated to lift the weight of the aircraft into the air. Most airplanes are equipped with extendible flaps that cause either increased wing chord and area (low aspect ratio), increased camber, or both. This permits greater lift and weight bearing at lower speeds. Were it not for these devices, the lengths of runways at international and military airports would be considerably longer. Helicopters, of course, can take off straight upward and do not require a take-off roll. This is accomplished essentially by attaching the engine to a rotating wing or horizontal propeller.

On the other hand, animal flyers must take off, fly, and land solely by using the lift and thrust generating capabilities of their wings. As we have noted several times, birds have the separate and independent use of the hindlimbs, a luxury not present in bats or pterosaurs. Many birds, such as ducks, albatrosses, and the like, run (or swim) for a distance while flapping their wings, until their wings are able to lift them into the air. Other birds are capable of taking flight directly from the perch or ground.

All bats launch by releasing their hold from the roost or resting site. Some open their wings and accomplish several wing beats before releasing their grip. Free-tailed bats (Molossidae), as a group, have wings of moderate to very high aspect ratios that require faster than normal air speeds to become airborne. Species such as the Greater Mastiff bat (*Eumops perotis*) select roosting sites that are 10 to 15 metres above the ground. When these bats launch, they free fall five to six metres to gain airspeed before they unfurl their wings to take flight. Another rather spectacular instance of free falling, not associated with launching, is used by the Mexican Free-tailed bat (*Tadarida brasiliensis*–Molossidae) upon returning to their roost at Carlsbad Caverns, New Mexico.

These bats approach the cave entrance at about 300 to 400 metres altitude. When they are directly over the entrance, they fold their wings and free fall to about two to three metres above the ground, then snap open their wings and shoot into the cave.

Many bat species are able to take off from the ground (or water surface) by beating their wings until they are airborne. Some ground-foraging species such as the Pallid bat (*Antrozous pallidus*–Vespertilionidae) and the Common vampire bat (*Desmodus rotundus*–Phyllostomidae) regularly take flight by launching from the ground. Vampires do this by moving the folded wing through a typical powerstroke. When the forearms contact the ground, the bat is catapulted into the air. Some forward thrust is gained in the recovery stroke, and with the next powerstroke they are fully airborne.

Landing

The termination of flight is another critical manoeuver for flyers. Whereas take-off occurs under ever increasing airspeeds, landing occurs at ever decreasing airspeeds to a point of stall when the wing will no longer support the weight of the flyer. Normally the wing stops flying at the desired landing point. Airplanes and some birds approach the landing point at a low glide angle, but high angle of attack and low airspeed. Airplanes, again, utilize mechanical structures such as flaps to increase the chord (camber) of the wing to enhance lift at these low speeds. Birds utilize the alula (feathered thumb, see discussion above) as a movable appendage in front of and slightly above the leading edge of the wing. With this structure, they are able to hold or channel the boundary layer of air on top of the wing at higher angles of attack than would be possible without such a structure. Recall that at high angles of attack the boundary layer starts to peel away from the rear portion of the airfoil until the stall occurs. The alula permits higher, stall-free, angles of attack and consequently greater lift at low airspeeds. Large jetliners have similar devices along the leading edges of their wings.

Bats do not normally alight on the ground. Instead, they must land on the ceiling of caves or on branches of trees. Large, tree-dwelling flying foxes (Pteropodidae) land by ungracefully crashing onto the branches or clumps of their companions near the roost site. Once they have landed, they simply crawl to their roosting space and hang upside down. Most bats either hover at the desired landing spot, grab hold, and swing into the typical upside down posture, or some species perform an aerobatic somersault in mid-air in order to gain a holdfast.

FLIGHT MUSCULATURE

The power required for bat flight, like any other mode of animal locomotion, is generated by pairs of muscles or muscle groups arranged in such a way that their actions are antagonistic. This antagonism is required because all muscles are only capable of contracting. These muscles are anchored to relatively immobile attachment sites (origin) and attach (insert) somewhere along a lever arm, usually across a pivotal joint or fulcrum. One pair of muscles or muscle group moves the lever arm in one direction, whereas the antagonistic muscles move it in the opposite direction.

Power and recovery muscles

The flight muscles that pull the wing of the bat through the powerstroke are located on the chest and upper part of the humerus (Fig. 4.4A). The muscles that lift the wing through the recovery stroke are located on the upper part of the back (Fig. 4.4B). The mass of these muscles is located on the body and thereby contributes to the stability of the centre of gravity and does not add to the kinetic weight of the wing proper.

Four large muscles act on the humerus during the powerstroke (Fig. 4.4). These are: M. pectoralis (origin: clavicle and sternum, insertion: proximal humerus); M. clavodeltoideus (origin: clavicle, insertion: proximal humerus); M. serratus anterior (origin: broad band from mid-section ribs one to four, insertion: antero-medial portion of scapula); and M. subscapularis (origin: ventral surface of scapula, insertion: proximal humerus). Most of these muscles act directly on the humerus to drive it downward during the powerstroke. The pectoralis is by far the largest of these, weighing approximately 65 per cent of the combined weight of the other three. However, in relation to the total body weight the pectoralis muscle of bats consistently comprises less than ten per cent of the total weight, regardless of the overall size of the bat. In birds, pectoralis weight/total weight varies considerably and is generally higher than in bats; 12 to 22 per cent among flycatchers, 14 per cent in the Black vulture, and 21 per cent in the Bobwhite quail.

Five muscles or muscle groups are involved in the recovery of the wing (Fig. 4.4B). These are: [trapezius group] M. acromiotrapezius, and M. spinotrapezius (origin: cervical and thoracic vertebrae, insertion: medial surface and vertebral border of scapula); M. rhomboideus (origin: thoracic vertebrae one through seven, insertion: medial border of scapula); [supra-
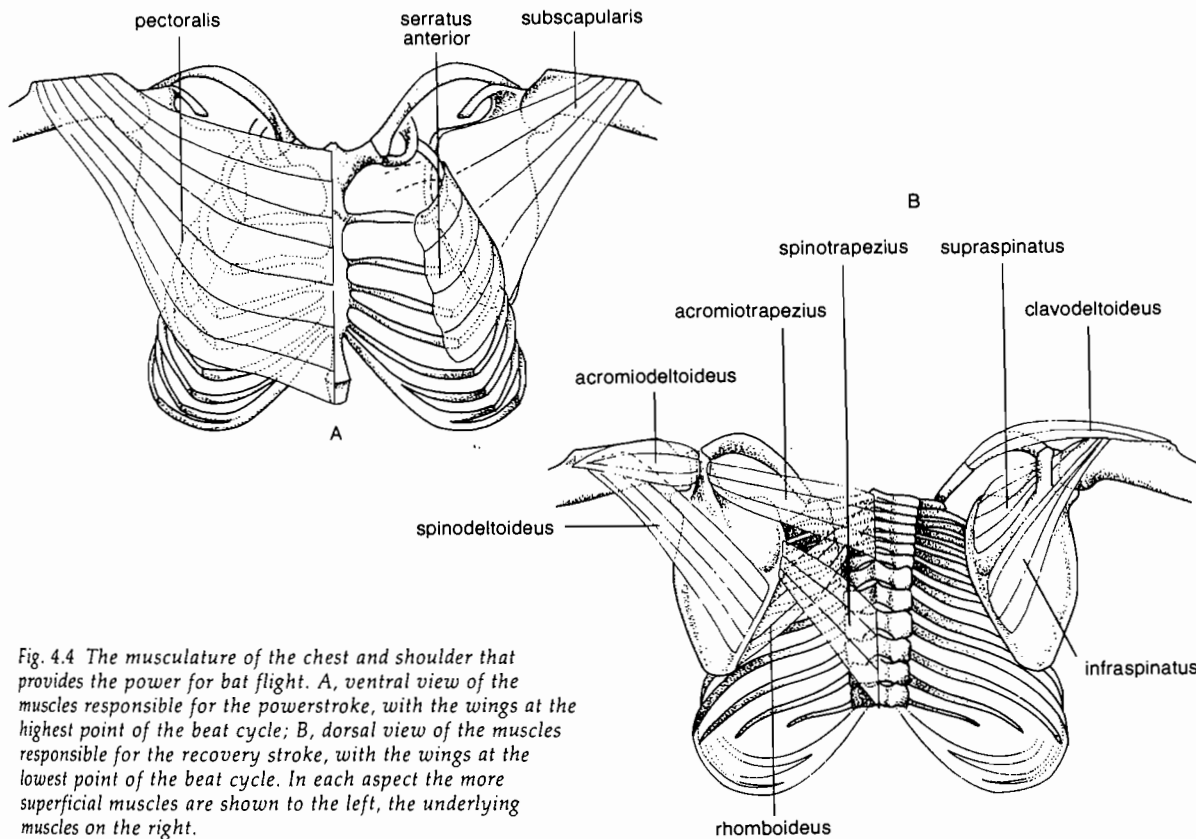
Fig. 4.4 *The musculature of the chest and shoulder that provides the power for bat flight. A, ventral view of the muscles responsible for the powerstroke, with the wings at the highest point of the beat cycle; B, dorsal view of the muscles responsible for the recovery stroke, with the wings at the lowest point of the beat cycle. In each aspect the more superficial muscles are shown to the left, the underlying muscles on the right.*
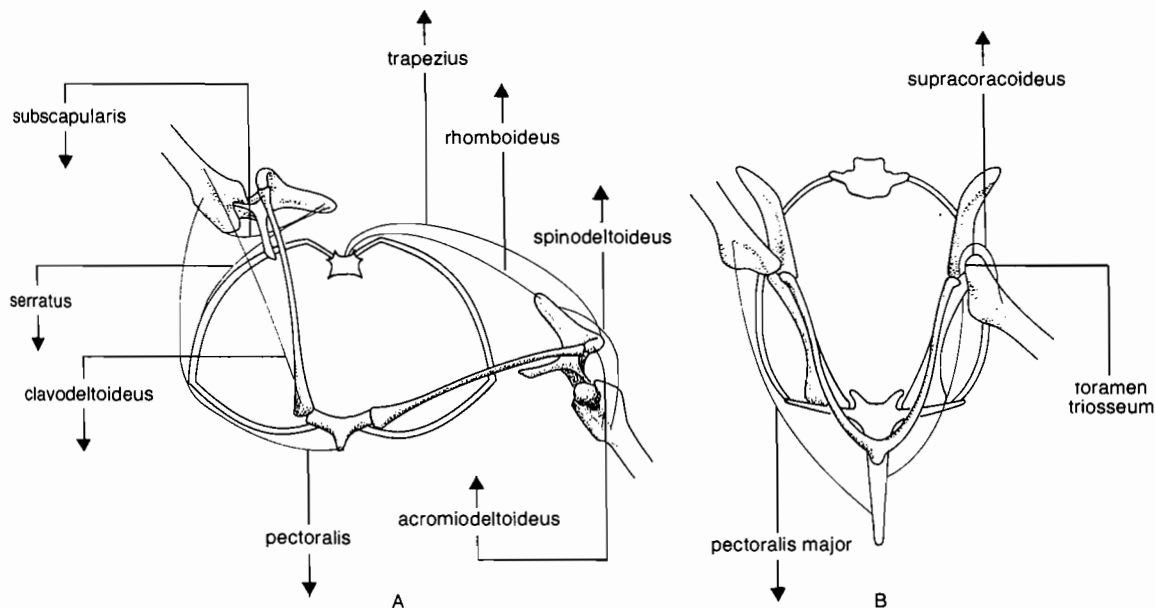

Fig. 4.5 *The action of the major flight muscles in A, bat, B, bird in anterior view. The muscles responsible for the powerstroke (↓) are indicated to the left, those for the recovery stroke (↑) to the right.*

scapular group] M. infraspinatus (origin: lateral surface scapula, insertion: proximal humerus) and M. supraspinatus (origin: medial surface of scapula, insertion: proximal humerus); [deltoideus group] M. acromiodeltoideus (origin: spine of scapula, insertion: proximal humerus) and M. spinodeltoideus (origin: vertebral border of scapula, insertion: proximal humerus). These muscles are smaller, in overall size, than those which act during the powerstroke. Most act directly on the scapula and indirectly on the humerus.

To illustrate how these muscles function during the wing beat cycle, we begin as the wing is being recovered (Fig. 4.5A). The recovery muscles on the back have been stretched, and the scapula has been
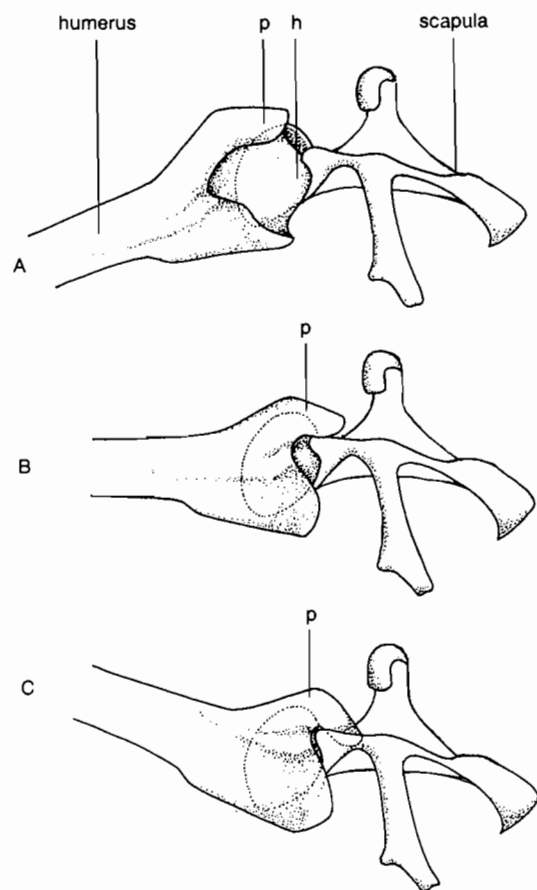

Fig. 4.6 *Anterior view of the right shoulder joint of the bat* Cheiromeles torquatus (Molossidae). *The projection (p) locks the humerus and scapula during the upper part of the wing beat cycle. A, Wing lowered, the humerus folded back towards the body so that its head (h) can be seen articulating with the scapula; B, wing horizontal, the humerus extended slightly away from the body; C, wing raised and fully extended, the projection (p) articulating fully with the upper surface of the scapula.*

tilted outward and downward. The muscles anchored to the thoracic vertebrae and inserted on the scapula contract to rock the scapula back. At the same time, the muscles anchored to the scapula and inserted on the proximal humerus contract to raise the humerus which carries the wing upward. The upward inertia of the wing being raised eventually rocks the scapula upward. At this point, the serratus anterior (a powerstroke muscle) is stretched. In some bats, there is a special process on the proximal humerus that contacts and locks onto the scapula (Fig. 4.6). The stretching of the serratus anterior along with the humerus/scapula contact act as a shock absorber.

The serratus anterior is the first of the powerstroke muscles to contract; its contraction stops the upward inertia of the wing in the recovery stroke and starts the powerstroke (Fig. 4.5). Soon after the serratus anterior contracts, the other powerstroke muscles contract and drive the wing downward.

Although the flapping flight of bats generally resembles that of birds, the arrangement of the flight muscles in birds further illustrates the marked evolutionary differences between these two groups of flyers (Fig. 4.5B). Whereas bats, and presumably pterosaurs, utilize antagonistic groups of muscles located on the chest (power) and back (recovery), respectively, birds have both power and recovery muscles (still antagonistic) located on the chest. In addition, birds utilize fewer muscles to accomplish the wing beat cycle. These muscular differences are also reflected in the skeletal systems of birds. The sternum is massive and strongly keeled in birds; also, the clavicles (wishbone) and coracoid bones are large (Fig. 4.7B). On the other hand, the scapula is rather reduced and does not play an important role in the wing beat cycle. The position and function of the large pectoralis muscle is similar to that described for bats. The recovery of the wing of birds is accomplished by the M. supracoracoideus (origin: keel of sternum, insertion: top of proximal humerus). It is the rigging of this latter muscle that is peculiar. From the sternum, the muscle passes through a hole (foramen triosseum) in the shoulder girdle, formed by the clavicle, coracoid, and scapula, to an attachment on the upper surface of the humerus.

The basic differences in the anatomical aspects of birds and bats no doubt reflect their different evolutionary histories. Both groups originated from reptiles. However, bats (mammals) are the descendants of the therapsid reptiles that departed early from the stem reptiles. On the other hand, birds and pterosaurs evolved from diapsid reptiles (including dinosaurs and crocodiles) that were a later, relatively more specialized group. Although different ancestry may account for some of the anatomical differences, it is
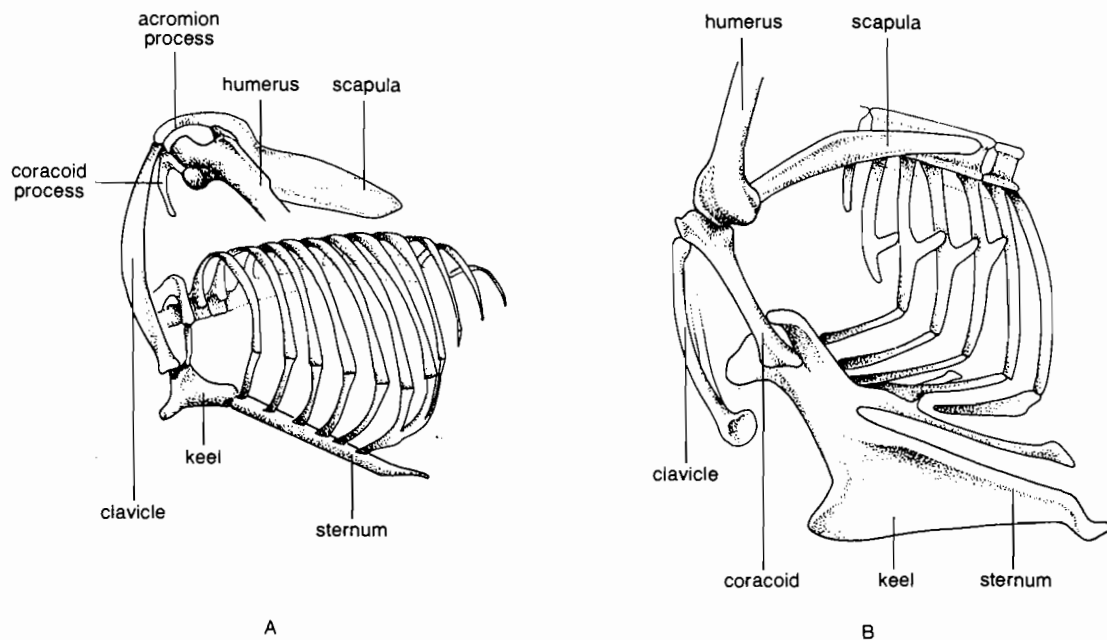
Fig. 4.7 *Lateral view of the pectoral skeleton of A, bat, B, bird. Birds have a strong coracoid, a slender clavicle and a massive sternum; in bats the clavicle rather than the coracoid supports the scapula and the sternum is much less substantial.*

more likely that the retention or further development of bipedalism by birds has had a marked impact on the nature of their flight morphology. Launching from trees or other high places would seem to require the modification of a quadrupedal morphology; that is, limbs operated by both chest and back musculature. Presumably, flight developed in these animals (bats and pterosaurs) by way of a gliding stage. The fact that birds and pterosaurs, with their markedly different flight morphologies, are more closely related to each other than either is to bats would seem to corroborate this notion that flight morphology is associated with bipedal versus quadrupedal launching.

Control of the wing

In order to overcome the inertial forces at the end of the powerstroke and recovery stroke, the wings of flying animals must be lightweight. The thin, pneumatic bones of birds and pterosaurs and the long, slender bones of bats are adaptations for this purpose. In addition to being lightweight, the structural (skeletal) components of the wing must be able to withstand the buckling forces generated by air pressure under the wing during the powerstroke. These buckling forces are focused at the elbow and wrist in all flying vertebrates and at the finger joints of bats and pterosaurs. In most vertebrates, flexible

joints are supported by heavy bindings of tough fibrous ligaments and muscles. However, in the case of flying vertebrates with critical weight constraints, heavy muscular and tendinous bulk must be minimized. Thus, joint strength in the wings of vertebrates is accomplished by articular modifications of the joints themselves so that movement is restricted (locked) to those planes (horizontal in most cases) that are perpendicular to the buckling forces.

In bats, the elbow joint is designed in such a way, with deep grooves and bony flanges, that the joint opens and closes in the horizontal plane. Some bats have refined this arrangement by angling the grooves and flanges so that as the joint opens (extends) it tightens or locks in much the same fashion that a screw tightens as it is turned down. The wrist joint is a complex articulation with many carpals interposed between the distal portion of the forearm and the digits. Normally, this joint permits a wide range of movements. In bats, the wrist joint is especially complex in that it must resist buckling as well as allow the co-ordinated movement of the digits. Thus, the carpals are broadened, reduced in size, and articulated in such a manner to permit movement in a horizontal plane similar to that of a folding fan. Although bats have reduced the role of muscles in bolstering joints, the wing still must be controlled by muscular actions. Bats and birds have overcome some of the problems associated with muscle mass and
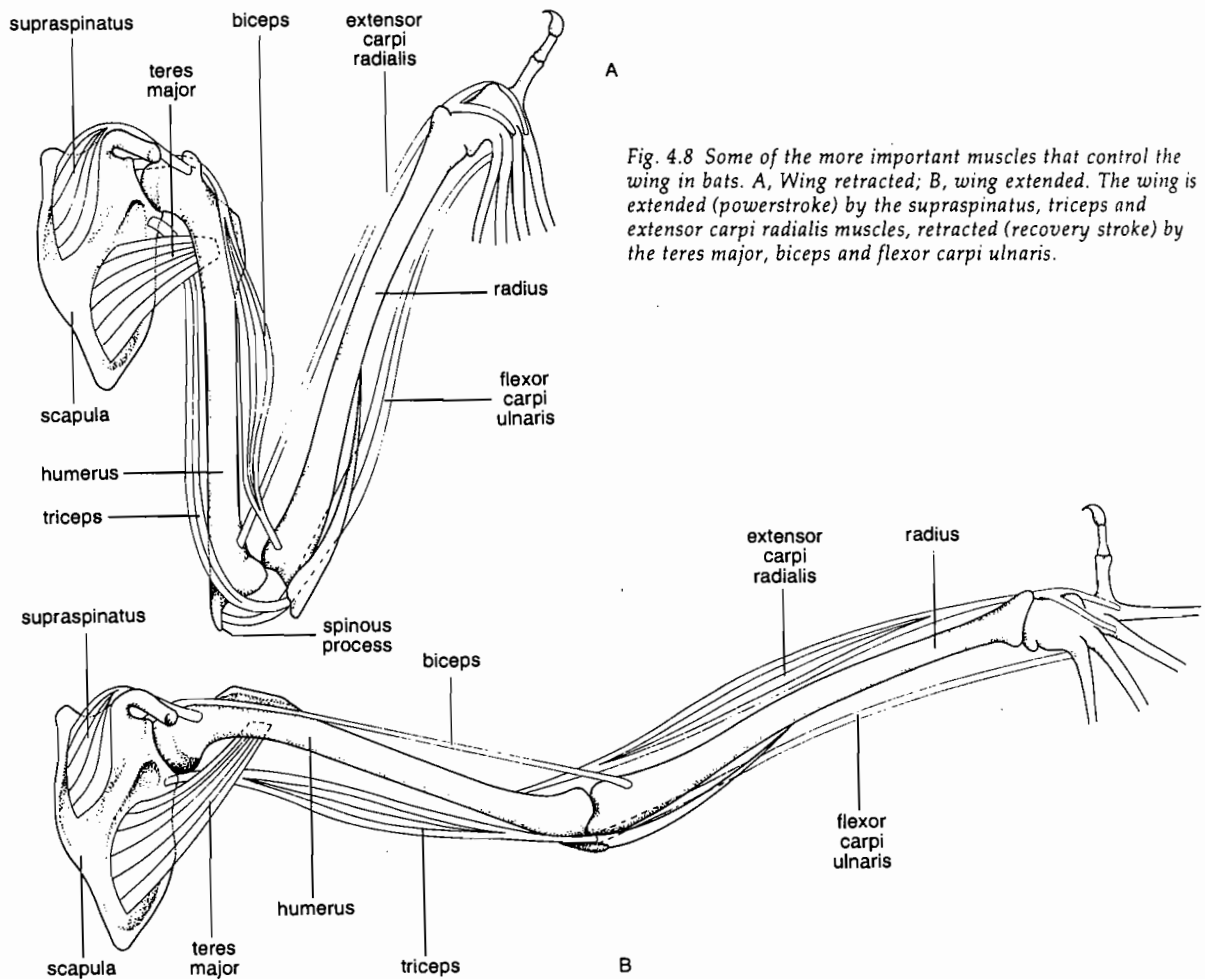
Fig. 4.8 Some of the more important muscles that control the wing in bats. A, Wing retracted; B, wing extended. The wing is extended (powerstroke) by the supraspinatus, triceps and extensor carpi radialis muscles, retracted (recovery stroke) by the teres major, biceps and flexor carpi ulnaris.

weight by reducing the size of muscles and restricting the heavy belly portions of muscles to regions close to the centre of gravity. These muscles operate by way of long, thread-like tendons that attach to and control movement in various wing components (Fig. 4.8). In addition, these muscles are arranged in such a way that the action of one or several muscles causes a series of automatic actions in the outer portions of the wing.

The automatic nature of wing control in bats can be illustrated by examining the action between the antagonistic biceps and triceps muscle groups. These two muscle groups attach in much the same manner as in the human arm: M. biceps brachii (origin: two heads attached to coracoid process of scapula, insertion: flexor fossa on proximal radius) and M. triceps brachii (origin: lateral and medial heads attached to posterior surface of proximal humerus and long head attached to lateral border of scapula, insertion:

olecranon process, rear of proximal radius). During the powerstroke, the triceps contracts and opens the elbow joint (extends the radius). At the same time, the biceps pulls and rotates the humerus forward; the contraction of the triceps also enhances the tension of the biceps. When the triceps relaxes at the bottom of the powerstroke, the elasticity of the tendon of the biceps allows the humerus and radius to be flexed (elbow joint closed) passively. The respective actions of these two muscle groups on the humerus and radius cause other automatic actions in the outer wing. The extension of the radius by the triceps triggers the action of two highly inelastic and tendinous muscles. These are: M. extensor carpi radialis longus (origin: lateral epicondyle of distal humerus, insertion: proximal portion of first and second metacarpals) and M. extensor carpi radialis brevis (origin: lateral epicondyle of distal humerus, insertion: proximal portion of third metacarpal). As the elbow joint

opens, the origin of these two muscles on the distal humerus moves away from the wrist. This action causes the tendons of these muscles to pull (extend) on the first, second, and third fingers and thereby open (extend) the dactylopatagium. Thus, the triceps effects the full opening of the wing during the powerstroke.

The action of the biceps has a similar automatic but reverse, effect on muscles in the outer portion of the wing during the recovery stroke. This involves the M. flexor carpi ulnaris (origin: spinous process of medial epicondyle of distal humerus, insertion: pisiform carpal that articulates with fifth metacarpal). As the radius and humerus are flexed (elbow joint closed) during the recovery stroke, the origin of the M. flexor carpi ulnaris is moved away from the wrist. This action causes the tendon of this muscle to pull on the fifth metacarpal and thereby partially collapse the dactylopatagium. In some bats, such as molossids, mormoopids, and other assorted species, a spinous process on the distal humerus may be greatly elongated causing the origin of the M. flexor carpi ulnaris to rotate through a wider arc and thereby enhancing the automatic nature of wing flexion during recovery. Bats with this adaptation have high performance wings and are mostly swift flyers. Other, less automatic muscles, assist in the dextrous control of the wing during the wing beat cycle.

As we have noted throughout, the anatomical structure of the avian wing is quite different from that of bats. Nonetheless, birds utilize various automatic devices to control the outer portion of their wings. Recall that the radius and ulna are large bones in the wing of birds. These two bones and their associated articulations with the humerus (proximally) and the fused carpometacarpal (distally) act as a flexible parallelogram. The extension and flexion of this skeletal complex automatically extends and flexes the outer wing.

FLIGHT STYLE AND WING SHAPE

Much speculation has been advanced concerning wing shape and flight style of bats, yet only a handful of species has been studied critically in this regard. Part of the reason for this is the secretive nocturnal habits of bats that makes their direct observation difficult. Other reasons concern the high cost of high-speed motion picture cameras, film, wind tunnels, and other laboratory-based equipment. In addition, bats must be captured, brought into, maintained, and trained to fly in the laboratory under controllable light and airspeeds.

Morphometric studies of many species, preserved in museum collections throughout the world, have shown that bats possess a wide variety of wing sizes and shapes. Wing size appears to be directly correlated with body size. However, wing shape appears to be independent of overall body size. The shape of the wing is controlled by the lengths of the various skeletal components of the wing. Most past studies concerned with the shape of bat wings have overly relied upon the silhouette or aspect ratio of the wing. These studies portray bat wings as low, intermediate, or high in aspect ratio. Certainly, the overall shape or silhouette may be important from the standpoint of such aerodynamic factors as wetted surface area or wing loading. However, the internal composition of the wing (length of various skeletal components) determines the camberability and ultimately the dynamics of lifting potential and manoeuverability.

Generally speaking, bats with relatively short, broad wings (low aspect) are slow flyers. The breadth of the wing chord permits high lift and high weight-bearing potential. Nearly all frugivorous bats (pteropodids and phyllostomids) and many insectivorous species have low aspect wings. In addition, wings with low aspect apparently permit highly manoeuverable flight styles in and around a tangled environment. On the other hand, bats with long, narrow wings (high aspect) are generally swift flyers. Wings of this sort require fast airspeeds and have low weight-bearing potential. Also, these high aspect wings are less capable of manoeuverability in confined spaces. Molossid bats have the highest aspect wings, and they are often cited as the epitome of high performance flight. However, other bats such as noctilionids, mormoopids, and some emballonurids also possess wings of high aspect; not all of these are noted for swift flight.

In reality, every bat family has a distinctive wing shape. The shape of the wing is better understood by examining its functional areas; that is, plagiopatagium and dactylopatagium. The wings of pteropodids (Megachiroptera) are unique among bats by having a broad plagiopatagium and dactylopatagium. In particular, the lengths of the metacarpals of digits three to five are nearly equal or subequal. Also, all of the phalangeal elements are nearly equal in length. This degree of isometry does not occur in any other family of bats. The functional results of such a wing should be a high degree of camberability and consequently high lifting potential. As noted earlier, the Megachiroptera include the largest bats and most are heavy bodied. None is thought to be capable of hovering, but *Pteropus*, and perhaps others, frequently glide for long distances.

The wing shape of rhinopomatids is rather curious.

These bats have an extremely high aspect plagiopatagium and a rather short, broad, (low aspect) dactylopatagium. Overall, the wing is below the average aspect ratio of all bats. The flight style of Mouse-tailed bats (*Rhinopoma*) has been described as a series of alternating flutters and glides as well as swift in open country. This versatility would seem to agree with the flight potential such a wing should possess.

The aspect ratio of the plagiopatagium in emballonurids is only slightly lower than that of rhinopomatids. However, the dactylopatagium of this family is extremely long and narrow. Some species, such as those of the genus *Taphozous*, are fast flyers, whereas most of the other species are capable of rather slow, highly manoeuverable flight.

Wing shape in the Rhinolophidae, Hipposideridae, Nycteridae, and Megadermatidae is quite similar and varies only in the relative proportions of the digital elements. In these families, the plagiopatagium is very short and broad. The dactylopatagium is also low in aspect ratio. The terminal (second) phalanx of the third digit is peculiar in these families. In proportion to the other elements of this finger, this element is very long. In addition, it is permanently bowed and the wing membrane, captured in this bow, is always taut, even in preserved specimens. The articulation of this phalanx with the first phalanx is extremely mobile and may somehow enhance the thrust potential of the wing-tip.

Noctilionids, mormoopids, and phyllostomids have wings in which the plagiopatagium is rather low in aspect. The third finger of these families is very long; the wing chord (length of the fifth finger) also is rather long. In noctilionids and mormoopids, the overall silhouette is high in aspect. In the phyllostomids, the overall shape is just below the average aspect ratio of all bats. In two phyllostomid subfamilies (Glossophaginae and Carolliinae), the plagiopatagium is quite short and broad and the bulk of the wing is composed of the long wing-tip. These bats, especially the glossophagines, are nectarivorous (nectar-eating) and are capable of sustained hovering flight. Other phyllostomids also are capable of varying degrees of hovering. The wings of phyllostomids are capable of bearing considerable weight. Some of the frugivorous species of *Artibeus* and *Phyllostomus* are frequently observed carrying fruits that weigh one-half to two-thirds their body weight. The large carnivorous species such as *Vampyrum spectrum* are capable of capturing and carrying away adult parrots. In addition, the females of all phyllostomids carry large full-term embryos, and large newborn are frequently carried by the foraging mother for several days after birth.

The Vespertilionidae, as a group, fall near the average of all bats with regard to wing shape. The plagiopatagium and dactylopatagium are generally short and broad. However, there is a wide array of wing shapes and, presumably, flight styles. Some species, such as *Otonycteris*, *Kerivoula*, *Miniopterus*, *Lasiurus*, and *Eudiscopus*, have wing-tips with relatively high aspect ratios. The metacarpals of digits three through five are usually very long comprising 50 to 80 per cent of the length of the respective digit.

The wings of molossid bats are extremely long and narrow (high aspect). The majority of this wing shape is contributed by the long, narrow dactylopatagium. The terminal phalanges of digits three to five are very short, and the fifth metacarpal is extremely short compared to those of digits three and four. As we noted above, molossids are generally swift flyers. Their wing beat cycle is very rapid, shallow, and highly stereotypic; that is, without much variation. The humerus of these bats has a secondary articulation with the scapula which serves to restrict the vertical movement of the wing, and the automatic flexing and extending devices in the outer wing are highly developed (Figs. 4.6 and 4.8). Molossids usually forage in open areas that are unencumbered by obstacles. On the ground these bats are virtually helpless and must crawl up a vertical surface in order to launch into the air.

PHYSIOLOGY OF FLIGHT

Thus far, we have discussed the various anatomical and aerodynamic aspects of bat flight. Closely associated with these parameters are the physiological and energetic prerequisites of this highly specialized mode of locomotion. Just as there are parallels and contrasts between birds and bats with respect to anatomical and aerodynamic adaptations for flight, there are similarities and differences between these two groups of flying vertebrates with regard to their physiological adaptations for aerial locomotion.

There is considerably more information concerning the energetics of bird flight than there is for bat flight. Although there is a wealth of information regarding other aspects of chiropteran physiology, the flight physiology of only three bat species (*Phyllostomus hastatus*, *Pteropus alecto*, and *Pteropus poliocephalus*) has been studied in any detail. Again, a large part of the problem of investigating chiropteran flight physiology involves getting the experimental subjects to fly naturally under controlled circumstances (in laboratory-based wind tunnels) with an array of physiological probes, encumbering leads, and other gadgetry. For example, monitoring ventilation and

oxygen consumption requires placing a mask over the face of the animal during flight activity. Birds accept these masks rather easily. However, with bats, difficulties arise because, in addition to breathing through the mouth and/or nose, they also emit their acoustic orientation sounds through the mouth and/or nose. Facial masks interfere with these orientation sounds and cause either abnormal flight or the animals refuse to fly altogether. Also, the weight of monitoring equipment that must be borne by the animal in flight limits the size of species that can be studied. Thus, it should be no surprise to find that the three species that have been studied are large species with low aspect (high weight-bearing) wings that either rely little on acoustic orientation (*Phyllostomus*) or do not use it (*Pteropus*).

Basic energetics

The energy to do the mechanical work accomplished by the muscles of any animal is derived from the oxidation of some fuel (food), either carbohydrate or fat. These contain chemical energy in varying quantities and qualities. During the oxidation process (in muscle cells), about 20-25 per cent of the stored chemical energy is released to accomplish mechanical work; the remaining 75-80 per cent is released as excess heat. Compared to other modes of locomotion, flight activity is extremely expensive in terms of its energetic requirements.

Flight muscles of birds and bats may be specialized to operate on either carbohydrates or fats; in some cases, a muscle may be mixed. Carbohydrates must be stored in a hydrated (dissolved in water) form. Therefore, for a given amount of energy, the mass (weight) of carbohydrate fuel that must be lifted, in flight, is approximately eight times that of an equivalent unit of fat. On the other hand, oxidation of a unit of fat produces about twice the energy yield of an equivalent unit of carbohydrate. In addition, fat does not require hydration. In terms of mass per unit of energy, fat contains 0.11 milligrams per calorie (mg/cal). By comparison, honey contains about 20 per cent water and about 0.33 mg/cal; nectar contains about 60 per cent water and about 0.67 mg/cal; and glycogen contains 73 per cent water and 0.88 mg/cal. Thus, fat is a more compact, energy economical fuel.

In addition to the mechanical apparatus (skeletal and muscular) required for flight, the complete animal must have supporting systems (respiratory and circulatory) capable of delivering fuel and oxygen to the cells of flight muscles as required and able to remove and dispose of various chemical by-products, such as lactic acid and carbon dioxide, and excess heat produced in the metabolic (oxidative) process.

Flight exertion

Two general types of flight exertion, 'cruise' and 'sprint,' may be distinguished. Under prolonged cruising flight, oxygen must be absorbed in the respiratory organs and delivered to the flight muscles at the same rate as the muscles are using it. Similarly, in the steady state demand, fuel must be removed from storage and delivered to the flight muscles at the rate of use, and metabolic wastes (including excess heat) must be removed at the rate at which they are produced. These equalities determine the minimum capacities of the respiratory, circulatory, and heat disposal systems required to permit continuous, prolonged flight. Fats are consumed in cruising flight and cellular metabolism (oxidation) is aerobic (steady state oxygen utilization).

In sprinting flight, the power output and demand of the flight muscles temporarily exceeds the capacity of the supporting systems to deliver oxygen and fuel, and remove chemical wastes and excess heat. Under these circumstances, which can prevail for only short periods of time, the burst of activity of the flight muscles quickly depletes the small fuel reserves in the muscle cells. Carbohydrates are consumed during these short bursts and cellular metabolism (oxidation) is conducted under anaerobic (without oxygen) conditions. Since this activity exceeds the supply and demand of the flight muscles, they accumulate waste by-products (including excess heat) and develop an oxygen debt. This deficit must be cleared by a subsequent increase in oxygen consumption; excess heat is absorbed by a temporary rise in body temperature.

Ventilation rate

The high metabolic requirements of flight place heavy demands on the ventilatory apparatus of bats. *Phyllostomus hastatus* (Phyllostomidae) and *Pteropus alecto* (Pteropodidae) maintain a rigid 1:1 synchronization between ventilation and the wing beat cycle; *P. hastatus* with ten cycles per second. The phase relationship is such that inspiration is always associated with the powerstroke; expiration occurs during the recovery stroke. [It is of interest to note here that *Phyllostomus hastatus* emits its ultrasonic vocalizations during the expiratory phase of ventilation.] As a result of the 1:1 synchronization of ventilation and the wing beat cycle, there is an abrupt increase in the breathing rate at the initiation of flight and a similarly abrupt decline as soon as the bat lands (Fig. 4.9). In *Phyllostomus hastatus*, this amounts to approximately 7 cm^3 of oxygen per gram body weight per
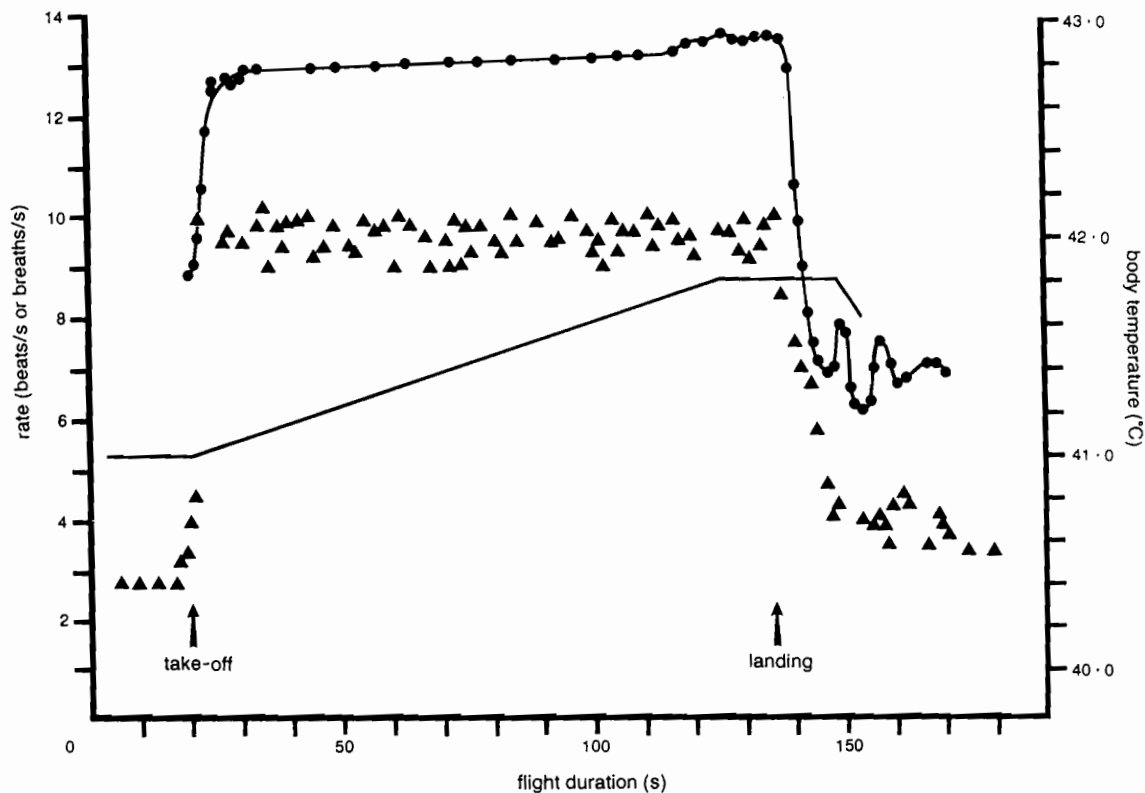
Fig. 4.9 Physiology and energetics of flight in Phyllostomus hastatus (Phyllostomidae). Top line with dots is cardiac response (heart beats/s) showing sudden increase in heart rate at the start of flight, constant rate during flight, and rapid return to pre-flight levels upon landing. Triangles show respiratory rate (breaths/s) during the same flight. Straight line in middle of graph shows the increase in core body temperature before, during, and after the flight. Ambient temperature during flight trial was 25° to 26° C. (Thomas & Suthers, 1972).

hour (cm³g⁻¹h⁻¹) before flight to about 27 cm³g⁻¹h⁻¹ during flight.

The correlation of ventilation with wing beat has been examined in many bird species. Whereas some such as the pigeon seem to maintain a 1:1 synchrony, most others show considerable variability. The budgerigar (Melopsittacus undulatus) has a constant wing beat cycle (840 beats min⁻¹) at all flight speeds; its ventilatory rate varies continuously with changes in flight speed. In other species, several wing beats occur in one ventilation cycle.

In both Phyllostomus hastatus and Pteropus alecto, the ventilatory frequency and inspired tidal volume (amount of air entering and leaving the lungs) are dependent on airspeed and flight angle. Ventilatory frequency (and wing beat frequency) are inversely related to airspeed; both decline at higher airspeeds. On the other hand, inspired tidal volume increases with airspeed mostly as the result of the fact that more air is forced (rammed) into the lungs at higher speeds. The relationship is not surprising since the oxygen requirements and rate of gas exchange in the lung are higher at faster flight speeds. These two bat species are slightly below and above, respectively, the expected ventilation rates of birds of equivalent body size. Preliminary data suggest that these two species of bats are slightly less efficient at extracting oxygen from a particular unit of inspired air than are birds, and both appear to compensate by over-ventilating their lungs.

Heart rates

The high metabolic demands of flight require high rates of oxygen transport by the cardiovascular (circulatory) system. In-flight heart rates are known for only two species. In Eptesicus fuscus (body mass, 20 g), heart rate increases from 420-490 beats min⁻¹ (prior to flight) to 970-1097 beats min⁻¹ in flight of two to four seconds duration. During two-minute flights in a large room, the heart rate of Phyllostomus hastatus (body mass, 100 g) increases from an anticipatory pre-flight rate of 420 beats min⁻¹ to an average rate of 780 beats min⁻¹ in steady flight (Fig. 4.9). In both of

these species, heart rates return to the pre-flight rates within 10 to 20 seconds after landing. These values are only slightly higher than those observed for birds of equivalent body size and both are not substantially higher than heart rates of exercising terrestrial (non-flying) mammals. Thus, heart rate alone does not appear to account for the increased demands of oxygen transport during flight.

As we noted in Chapter 2 the hearts of bats are proportionately much larger than those of non-flying, terrestrial mammals of equivalent size. Although the cardiac output (stroke volume) has never been measured directly in either flying bats or birds, these values have been estimated. The stroke volume of *Eptesicus fuscus* has been estimated to be 1.08 cm³kg⁻¹ body weight and the minimum stroke volume of *Phyllostomus hastatus* has been calculated to be 1.9-2.2 cm³kg⁻¹ body weight. These values fall between those estimated for flying birds (2.7-3.4 cm³kg⁻¹) and deer mice (1.4 cm³kg⁻¹).

Since birds and bats (those studied) have similar rates of oxygen consumption and heart rates during flight and if, as the data for *Phyllostomus hastatus* suggest, their stroke volumes are lower, then bats must compensate by increasing the amount of oxygen transported by the blood. This is accomplished by raising the percentage concentration of red blood cells in the blood (high haematocrit). *Phyllostomus hastatus* has a blood oxygen capacity that is 40 to 50 per cent higher than that of either a typical bird or non-flying mammal and could, theoretically, transport 1.5 times as much oxygen per unit of blood flow as a bird or rodent. As we will note in Chapter 6 hibernating bats have the ability to regulate their haematocrit by storing red blood cells in the spleen during periods of non-activity. Although it is strongly suspected, it is not known whether bats can or do regulate their haematocrit between and during flight sorties.

Metabolic rate and cost of transport

The metabolic rate or power input is dependent on the body mass as well as on airspeed and flight angle. For birds, bats, and running mammals, metabolic rate is inversely correlated with body mass. Thus, the metabolic rate of a 100 g individual of *Phyllostomus hastatus* utilizes about 1.9 times more oxygen than does an 800 g *Pteropus alecto*. About the same relationship is found between bird species of equivalent body size (for example, budgerigar and seagull). Both birds and bats exceed the highest metabolic rates of running mammals by a factor of 2.5-3.0.

The cost of transportation is defined as the energetic cost of moving a unit of body weight over a given distance. The speed at which an animal can cover a given distance with the lowest energetic cost is its minimum cost of transportation. As might be expected, the minimum cost of transportation is also inversely related to body mass. Thus, *Phyllostomus hastatus* requires about twice the energy expenditure per unit of body weight to travel a given distance than does *Pteropus alecto*. Available data indicates that birds of comparable size are capable of a lower minimum cost of transportation than are bats. On the other hand, *Pteropus alecto* requires only one-fourth, and *Phyllostomus hastatus* only one-sixth the energy expenditure to cover a given distance than do walking or running mammals of comparable size. Thus, even though metabolic expenses of flight are high, the overall costs of this mode of locomotion are markedly lower than terrestrial forms of locomotion.

Fuel utilization

Relatively little is known concerning the utilization of carbohydrates and fats by flying bats. The data on *Phyllostomus hastatus* suggest a high reliance on carbohydrates. However, the flight sorties observed in the experimentation on this species were of relatively short duration in the laboratory and it is quite likely that, under these circumstances, they operated under carbohydrate oxidation. Other work has approached the problem of determining fuel preferences by bioassaying flight muscle tissues to determine enzyme activities. The activities of certain enzymes can be identified with aerobic processes (fat oxidation–cruising flight), whereas others are implicated in anaerobic processes (carbohydrate oxidation–sprint flight). Bats that have low aspect wings and make short dashing flights to capture insects might be expected to depend on carbohydrate utilization, whereas bats with high aspect wings and prolonged flight activity might be expected to rely more heavily on fat metabolism. No doubt this generalization will prove to be much too simplistic, but preliminary indications seem to support the notion. *Rhinolophus megaphyllus* and *Miniopterus schreibersii*, both with wings of low or moderately low aspect ratios, appear to rely heavily on carbohydrate, anaerobic metabolism. *Tadarida australis*, *Tadarida planiceps*, and *Eptesicus pumilus*, with relatively high aspect wings, seem to favour fat, aerobic metabolism. *Chalinolobus gouldii* and *Nyctophilus geoffroyi*, with wings of intermediate aspect ratio, are also intermediate in their preference of anaerobic or aerobic metabolism. There appears to be a strong correlation between food habits, activity patterns, and the relative utilization of carbohydrates and fats by the flight muscles. For example, the fruit-eating phyllos-

tomids such as the Big Fruit-eating bat (*Artibeus lituratus*) and the White-lined bat (*Vampyrops lineatus*) appear to rely heavily on carbohydrates. On the other hand, insectivorous species such as the molossid *Eumops dabbenei* appear to depend more on fat metabolism.

Temperature regulation

During flight activity huge quantities of excess heat are generated by the metabolic activity of the flight muscles. This heat must be channelled away effectively from the animal in order to avoid overheating.

Body temperatures (T_b) of active, temperate bat species, measured over a wide range of ambient (T_a) temperatures, indicate that flight T_b is directly related to T_a in all species studied. For example, flight T_b of *Pipistrellus hesperus* is about 22°C at a T_a of −5°C and 39°C when T_a is 30°C. Thus, it appears that at least these temperate species maintain a constant flight temperature, but one that fluctuates with ambient temperature. Similar results were found with tropical species *Phyllostomus hastatus* and *Pteropus alecto*. Deep-body temperatures of *Phyllostomus hastatus* before flight are about 41°C. This temperature rises markedly at the beginning of flight. Thus, regulated temperature is just below the upper thermal lethal (42-43°C) for the species.

There are several possible routes of heat loss in animals–evaporative cooling from the respiratory tract for instance, or through the skin. Measurements from *Phyllostomus hastatus*, the only data available, indicate that it channels about 14 per cent of the total metabolic heat load generated in flight through the respiratory tract. Other mammals such as dogs and ground squirrels lose about 40-60 per cent of their excess heat load across the respiratory tract. The value for *Phyllostomus* is comparable to those known for birds that dissipate 15-20 per cent of their heat load through the respiratory surfaces.

It is not too surprising to find that *Phyllostomus hastatus* loses most of its metabolic heat load by way of non-respiratory means during flight. By virtue of their flight membranes, bats have greater body/ surface areas than do small mammals and birds of comparable size. About 80 per cent of the total surface area of the Pallid bat (*Antrozous pallidus*) is contributed by the flight membranes. We have described earlier (Chapter 2) the structure of these nearly naked, thin membranes, and their rich vascular supply. For example, the Yuma myotis (*Myotis yumanensis*), dilates (expands) its wing capillaries at T_b's of 40-41°C. Similar vasodilation patterns have been reported for several species of flying foxes (*Pteropus*) and *Phyllostomus hastatus*. It is not known exactly

what proportion of a bat's metabolic heat load is dissipated through the flight surfaces, but this means would seem to account for a substantial portion of their heat loss.

ORIGIN OF BAT FLIGHT

A discussion of the early evolution and origin of bat flight can be nothing more than reasoned speculation. The fossil record has not provided much insight with regard to this evolutionary history. Until now, all identifiable fossil bats possess wings that are, without question, as refined as those of modern bats. It is conceivable, although unlikely, that the fossil record may one day produce the proto-bat or half-bat.

There can be little doubt that the impetus to develop flight in birds, bats, and pterosaurs was quite different. Throughout this chapter we have acknowledged repeatedly the marked anatomical differences between birds and bats. Ornithologists continually debate two theories for the development of flight in birds. There are those who support an arboreal theory that takes *Archaeopteryx* as its mainstay. The wing skeleton of *Archaeopteryx* is certainly intermediate between that of its supposed reptilian ancestors and modern birds. Other aspects of the skeletal anatomy of *Archaeopteryx* strongly suggest that it was not capable of the sort of powered flight possessed by modern birds. On the other hand, it may have been a proficient glider. Thus, in order to glide, *Archaeopteryx* is envisioned hopping about in trees. The point that seems to be overlooked is whether *Archaeopteryx* or its ancestor developed its wings in trees or while it was still on the ground. The ground-based, cursory theory of bird flight places the bipedal ancestors of birds on the ground. This theory seems less popular because it postulates the initial development of wings for some purpose other than flight (e.g., balancing structures used during fast bipedal locomotion or perhaps as insect catching devices). Whatever the case may have been, terrestrial bipedalism would certainly have freed the forelimbs for other purposes and it seems likely that birds started their quest for the skies from the ground.

Bats, on the other hand, have but one mode of locomotion–flight. The skeletal and muscular design of their wings is clearly a modification of the typical, quadrupedal, mammalian architecture. The occupation of arboreal niches by mammals and the relatively frequent occurrence of gliding among these mammals strongly supports the notion that the ancestors of bats were indeed arboreal quadrupeds that initially developed gliding ability. The predominance of insecti-

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vory among primitive mammals and living bats has added this further dimension to the chiropteran ancestry.

Gliding permits the development and refinement of the plagiopatagial (lifting) portion of the patagium. It does not require any special musculature other than the standard chest and back muscles typical of all quadrupedal mammals. The development of the power-generating hand portion of the wing eventually does require some specialization. However, the initial steps might have entailed no more than webbing between the relatively unspecialized digits. This, of course, would have enhanced the gliding surface area and perhaps provided some refinements for directional control. If such adaptations did provide these 'advantageous' qualities one might expect them to persist in descendants of those individuals in which they were originally developed. Living Colugos seem to be the successful beneficiaries of such ancestors.

Further refinements would have included the elongation of the fingers. Initially, this trend could have proceeded without serious problems. However,

digital elongation would have reached a point where it produced an ungainly and clumsy structure that required movement as a wing rather than a fixed gliding device. With successful transition through this critical stage of wing development, bats would have been well on their way to occupying an aerial niche. Further refinements would have concerned increased manoeuverability and/or speed.

Some bat biologists have suggested that these early bats passed through a hovering stage. Certainly, some bats possess the ability to hover. However, this flight style is anatomically specialized, requiring a high aspect tip and many automatic devices. Energetically, it is the most expensive style of flight. It seems highly unlikely that the generalized wing of early bats was capable of such an aerodynamically elite flight style.

Finally, there remains the question as to whether all bats (Megachiroptera and Microchiroptera) are the descendants of a single common ancestor that developed wings or if each of these two suborders is the result of the independent acquisition of wings by unrelated ancestors.