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Chiroptera

Volume 2:

Ulla M. Lindhe Norberg
The Flight of Bats

Uwe Schmidt
**Morphologie und Funktion der
sensorischen Systeme bei Chiropteren**

Hans G. Erkert
Aktivitätsperiodik der Chiroptera



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Autor / Authors

Professor
Dr. Hans G. Erkert
Universität Tübingen
Zoologisches Institut
Auf der Morgenstelle 28
D-72076 Tübingen
Germany

Professor
Dr. Ulla Lindhe Norberg
Dept. of Zoomorphology
Medicinareg. 18
S-41390 Göteborg
Sweden

Professor
Dr. Uwe Schmidt
Universität Bonn
Zoologisches Institut
Poppelsdorfer Schloß
D-53115 Bonn
Germany

Herausgeber / Editors

Professor
Dr. Jochen Niethammer †
Zoologisches Institut der
Universität Bonn
Poppelsdorfer Schloß
D-53115 Bonn
Germany

Professor
Dr. med Dr. phil. h. c.
Dietrich Starck †
Balduinstraße 88
D-60599 Frankfurt
Germany

Professor
Dr. Martin S. Fischer
Inst. f. Spezielle Zoologie u. Evolutions-
biologie mit Phyletischem Museum
Friedrich-Schiller-Universität
Erbertstr. 1
D-07743 Jena
Germany

Professor
Dr. Harald Schliemann
Zoologisches Institut und
Zoologisches Museum
Universität Hamburg
Martin-Luther-King-Platz 3
D-20146 Hamburg
Germany

Schriftleiter / Managing Editor

Dr. Michael Köhncke
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Germany

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Nachrufe / Danksagung

Altersbedingtes Ausscheiden, Krankheit und Tod haben in den vergangenen Jahren erhebliche Veränderungen in der personellen Betreuung von Band VIII (Mammalia) des Handbuches zur Folge gehabt.

Professor Dr. Jochen Niethammer, der die bereits erschienenen und geplanten Teilbände über die Systematik, Biologie und Ökologie der Chiropteren noch mit konzipiert und anfänglich auch mit betreut hat, konnte seit langem nicht mehr an der Vollendung dieser Publikationen mitwirken. Er war nach einem schweren Unfall bereits im Jahre 1991 dazu nicht mehr in der Lage und starb 1998 an den Folgen dieses Unfalls.

Jochen Niethammer war seit 1982 Mitherausgeber des Handbuches. Mit großem Engagement und dem ihm eigenen freundlichen Nachdruck hat er sich an der Arbeit am Handbuch beteiligt und hierbei in erheblichem Maße Kraft investiert. Auf Grund seiner umfassenden Kenntnisse der Säugetiere und seiner großen wissenschaftlichen Kompetenz hat er für das Handbuch eine sehr wichtige Funktion wahrgenommen.

Professor Dr. Dr. Dietrich Starck ist am 7. Oktober 2001 im hohen Alter von 93 Jahren verstorben. Bis in seine letzten Lebenstage hat er an der Arbeit am Handbuch und auch an dem vorliegenden Chiropterenband aktiv mitgewirkt. Die wissenschaftliche Qualität und die konzeptionelle Weiterentwicklung des Handbuches ist ihm immer ein außerordentliches Anliegen gewesen.

Seit 1964 hat sich *Dietrich Starck* der Herausgabe des Handbuches in allen seinen Bänden in der gesamten systematischen Breite dieses Wer-

kes gewidmet. Die vielen unter seiner Mitwirkung erschienenen Teilbände des Bandes VIII, einige sogar aus seiner eigenen Feder, legen ein unübersehbares Zeugnis für seine Arbeit und für seine Hingabe an diese Aufgabe ab. Über all die Jahre war *Dietrich Starck* mit seinem unglaublichen Wissen, seinen überragenden Erfahrung als Wissenschaftler aber auch als Herausgeber wissenschaftlicher Werke nicht nur der Garant für die wissenschaftliche Qualität der Beiträge, sondern Leitfigur für Autoren und Mitherausgeber. Er ist für das Handbuch wie für die gesamte deutsche Zoologie unersetzbar.

Der vorliegende Chiropteren-Band mit seinen drei Beiträgen wurde nicht mehr von Herrn *Professor Dr. Heinz Wermuth* als Schriftleiter für den Band VIII des Handbuches betreut. Seit 1963 war *Heinz Wermuth* für das Handbuch der Zoologie tätig, und zwar ebenfalls als Herausgeber aller Bände. Nach 1982 hat er sich von der Herausgebertätigkeit zurückgezogen, blieb aber bis zum Jahre 2000 für den Band VIII als Schriftleiter tätig. Fachwissenschaftliche Kompetenz und ein unerschütterliches Qualitätsbewußtsein für Inhalt und Sprache waren all die Jahre der Tätigkeit für das Handbuch die Grundlage seiner Fähigkeit, eingereichte Manuskripte in anspruchsvolle Druckvorlagen zu verwandeln.

Herausgeber, Schriftleiter und Verlag sind sich gleichermaßen bewusst, dass dem Handbuch der Zoologie mit diesen Wissenschaftlern außerordentliche Persönlichkeiten verbunden waren, denen ebenso wie den Autoren, mit denen sie zusammen gearbeitet haben, großartige Beiträge zur deutschen wissenschaftlichen Literatur zu verdanken sind. Ihre Verdienste sind unvergessen.

Vorwort

Der vorliegende Teilband 61 des Handbuches der Zoologie setzt die Schriftenreihe über die Chiroptera fort. Dies ist die zweite von drei Publikationen über Fledermäuse. 1994 erschien der Beitrag **Chiroptera: Systematics** (Teilband 60), für den *Karl F. Koopman* vom American Museum of Natural History, New York gewonnen werden konnte, einer der weltweit führenden Wissenschaftler auf dem Gebiet der Systematik der Chiroptera.

Herausgeber, Schriftleiter und Verlag schätzen sich glücklich, dass für den jetzt veröffentlichten Teilband drei Wissenschaftler als Autoren tätig waren, die wie *Karl F. Koopman* über ein großes Renommee in der Mammalogie verfügen:

Ulla M. Lindhe Norberg hat ihren Beitrag **The Flight of Bats** einem Gebiet gewidmet, das für das Verständnis der Biologie dieser Tiere von zentraler Bedeutung ist. Nach Behandlung der flugbiologischen Grundlagen befasst die Autorin sich mit der durch Gestalt und Abmessungen der Flügel sowie durch die Körpergröße bedingten Flugeigenschaften der Tiere, um dann unter diesen Gesichtspunkten ausführlich die einzelnen Familien der Ordnung vergleichend zu analysieren. Anschließend folgt eine ebenfalls vergleichende Darstellung der verschiedenen Ernährungsstrategien der Chiroptera und der mit ihnen vorherrschend verbundenen Flugeigenschaften, die anhand einiger Charakteristika der Flügel verständlich gemacht werden.

Uwe Schmidt ist der Autor des zweiten Beitrages mit dem Titel **Morphologie und Funktion der sensorischen Systeme bei Chiropteren**. Die Morphologie und Physiologie aller exterozeptiven

Sinnesorgane der Chiroptera werden vorgestellt, wobei jeweils die besondere biologische Bedeutung der einzelnen Systeme und ihrer Leistungen berücksichtigt werden. Naturgemäß nimmt die Darstellung des akustischen Systems mit seinen komplexen Strukturen und außerordentlich vielfältigen Eigenheiten einen breiten Raum ein, da Echoortung – die Entsendung und Verarbeitung hochfrequenter Laute – eine der wesentlichen Grundlagen der Biologie aller Microchiropteren und einiger weniger Macrochiropteren ist.

Hans G. Erkert beschreibt die **Aktivitätsperiodik der Chiroptera**. Die Angehörigen dieser Ordnung haben trotz der strikt nächtlichen Lebensweise unterschiedliche Aktivitätsmuster entwickelt. Der Beitrag geht auf die natürlichen Muster der Flugaktivität ein und untersucht den Einfluss exo- und endogener Faktoren auf die Flugaktivitätsmuster. Er behandelt den endogenen Ursprung der Circadianperiodik, die Ultradian- und Lunarperiodik sowie circannuale Rhythmen, letztere im Zusammenhang mit der Fortpflanzung und dem Winterschlaf. Die verschiedenen Differenzierungen der Aktivitätsmuster werden als Anpassungen verstanden, die unter dem Einfluss verschiedenartiger Ernährungsweisen und -strategien sowie unter dem Zwang zur Optimierung der Energiebilanz entstanden sind.

Die Publikationsreihe über die Ordnung Chiroptera wird mit dem Teilband 62 **Biologie und Ökologie der Chiroptera** fortgesetzt. Der Autor *Erwin Kulzer*, ein ausgewiesener Fachmann in dieser Materie, ordnet darin eine ungeheure Materialfülle, so dass sich schließlich aus den drei Teilbänden ein Bild ergibt, dass unsere Kenntnis der Chiroptera wiedergibt.

März 2002

Martin S. Fischer (Herausgeber)
Harald Schliemann (Herausgeber)
Michael Köhncke (Managing Editor)

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The Flight of Bats

Ulla M. Lindhe Norberg

1. Introduction

Bats are adapted to different niches, so they have to fly in different ways associated with different wing morphology. Natural selection may favour a wing design that minimizes a bat's cost of flight. The most efficient flight mode and optimal flight speed depend above all on habitat structure, foraging behaviour, choice of food, and size of prey, but the selection pressures for various demands are probably often conflicting, necessitating compromise solutions. Some bats hawk insects in the air in open spaces or among clutter, some glean insects, some take small terrestrial mammals or fish, and still others cling on vegetation to take fruit. Some species migrate or commute long distances. Foraging also requires a high degree of manoeuvrability in aerial-hawking insectivorous species, hovering ability in gleaners and nectarivores and load-carrying capacity in those flying with heavy prey; all these behaviours put different requirements on wing shape and size. Relations between aerodynamics, wing form and foraging strategy in bats have been treated in detail by Norberg, U. M. (1972 a, 1976, 1985, 1986 a, 1986 b, 1987, 1990), Norberg & Fenton (1988), Norberg & Rayner (1987), Thewissen & Babcock (1991), and Lindhe Norberg et al. (2000). Others have considered bat flight morphology as related to flight pattern and foraging behaviour (Aldridge & Rautenbach 1987, Baagø 1987, Findley et al. 1972, Lang & Chapin 1917).

2. The evolution of bats

The early evolution of bats is a great controversy in modern systematics. Some authors have suggested that the two bat sub-orders Megachiroptera and Microchiroptera have a diphyletic origin (e. g. Pettigrew 1986, 1991, 1995, Pettigrew et al. 1989, Smith 1977, Smith & Madkour 1980), whereas others consider them to be monophyletic (e. g. Baker et al. 1991, Simmons 1994, 1995, Simmons et al. 1991, Simmons & Geisler

1998, Thewissen & Babcock 1991, Wible & Novacek 1988). According to the hypothesis on diphyletic flying foxes (Megachiroptera), the Old World fruit-eating bats, share a common ancestor with primates and colugos (Dermoptera), whereas Microchiroptera, frugivores as well as animal-eaters, evolved much earlier from small, agile insectivores. Flight should then have evolved twice. Linnaeus originally included bats (Vespertilio) in the order Primates, and Gregory (1910) united primates, bats, tree shrews, elephant shrews, and flying lemurs in the superorder Archonta. The hypothesis on monophyly states that Megachiroptera and Microchiroptera share a common ancestor, which either was an insectivore (Jepsen 1970) or a dermopteran (Novacek 1986 and 1994, Novacek et al. 1988).

The principal characters used in the diphyletic story to separate the two bat groups are related to the visual neural (brain) system and to penis morphology. Megachiropterans share with primates (and colugos) a variety of complex details in the organization of the visual neural system not found in microchiropterans. A few characters related to flight also separate the two bat groups, such as a simple shoulder joint in Megachiroptera, whereas it is more complex in Microchiroptera (Strickler 1978, Vaughan 1959, Schlosser-Sturm & Schliemann 1995), and a difference in the ratio of the lengths of the metacarpal and first phalanx of the digits (Pettigrew et al. 1989). The upstroke kinematics during flight also are different in the two bat groups; megachiropteran bats fold their hand wings in the upstroke, whereas microchiropteran bats keep their hand wings extended and straight (Norberg, U. M. 1990). But this may be a consequence of the difference in the metacarpophalangeal ratios, which latter may be an adaptation to different demands in manoeuvrability and agility.

On the other hand, there are far more morphological similarities between the two bat groups than between megachiropteran bats and primates (Simmons 1995). Wible & Novacek (1988) identified six derived features in the cranium of the two bat groups, which are either unique or very unusual among mammals. Baker et al. (1991) listed 18 unique features of the postcranial musculoskeletal system shared by

Megachiroptera and Microchiroptera. There also are similarities in the fetal membranes (Baker et al. 1991), but the most remarkable derived similarities are in wing morphology (Norberg, U. M. 1969, 1970, 1972 a).

In both bat groups the highly elastic flight membrane is outstretched by the five digits. The third digit controls lateral camber (curvature), the fourth digit controls both lateral and anteroposterior camber, whereas the thumb and the fifth digit can be lowered and elevated to control anteroposterior camber. The second and third digits form a special, unique, convex unit making the leading edge of the hand wing rigid without particularly strong skeletal elements (Norberg, U. M. 1969). To reduce wing weight, the digits are extremely slender; in both groups they are shaped so that they have the largest diameters in those planes where the bending forces are largest but reduced width in the other planes. The end phalanges are cartilaginous and flexible to reduce peak tension forces, and the tips of the fourth and fifth digits are widened along the wing's trailing edge to reduce the risk of membrane rupture at its attachment to the digit tips.

The wing membrane attaches to the body along its side in most species, but in some, both among megachiropteran as well as microchiropteran species, the wing membranes of both sides meet and form an almost continuous surface over the back of the bat and attach to the body near the centre of the back. The tail membrane, uropatagium, is large in most animal-eating species but reduced in megachiropteran bats and also in most vegetarian microchiropteran species (Phyllostomidae). This reduction may be an adaptation to climbing and clinging in trees during foraging (Norberg, U. M. 1989, Norberg & Rayner 1987).

Some membrane muscles are unique to bats, such as *M. occipitopollicalis*, which runs along the leading edge of the arm wing and tautens the membrane anterior to the arm (propatagium), and *M. coracocutaneus*, which helps reinforce the membrane posterior to the arm (plagiopatagium) by anchoring the supporting network of elastic fibers to the axilla (Norberg, U. M. 1970 and 1972 a, Vaughan 1959). The occipitopollicalis muscle receives innervation from both the facial and cervical spinal nerves in the two bat groups; this dual innervation is unique among mammals (Thewissen & Babcock 1991). Both groups have several, almost identical, skeleto-muscular force-lever systems in the wings for increased mechanical performance (Norberg, U. M. 1970, 1972 a, 1972 b).

A question raised in the monophyletic-diphyletic controversy is whether wings or brain traits

evolved twice. Pettigrew (1991) presented these two options: 1) the primate brain features evolved twice, once in primates and once within a part of the bat lineage, or 2) wings evolved twice, once within the primate lineage (from which Megachiroptera should have evolved) and once in the line giving rise to Microchiroptera. But he eliminated at least two other possibilities (Simmons et al. 1991), namely, 3) independent convergent evolution in both the visual neural system and flight apparatus (probably unlikely) and 4) homology in both brain and wing systems, with subsequent reversal of brain traits in Microchiroptera.

Biochemical and molecular studies have provided support for the hypothesis that bats are monophyletic (Novacek 1994, Simmons 1995). When these and all morphological data are combined, the results suggest that Chiroptera are monophyletic and, hence, that flight in bats evolved once.

However, an additional problem is echolocation. All microchiropteran bats echolocate, whereas only a few megachiropterans do (species of *Rousettus*). *Rousettus* uses a quite different, simple system of echolocation with low frequency sound being produced by tongue clicks, not high-frequency laryngeal sound pulses as in microchiropterans. Study of the cochlear system (which sorts and processes sounds by frequency) of fossil skulls strongly suggest that extinct microchiropteran bats from Eocene could echolocate, but that its echolocation was not as advanced as that of modern microchiropteran bats (Habersetzer & Storch 1992). This suggests that the extinct microchiropterans did not depend entirely on echolocation but made use also of vision, prey-generated sound, or olfaction. If an early, common ancestor of bats could echolocate, then megachiropterans have lost this ability and the anatomical adaptations making it possible (e. g. Arita & Fenton 1997, Fenton et al. 1995). An other possibility is that there was an earlier ancestor than the eocene bats, from which both megachiropteran and microchiropteran bats derived, and which lacked the possibility of echolocation. The echolocation system in microchiropterans then may have originated later and become increasingly sophisticated as their flight became more manœuvrable and agile (Norberg 1989 & 1994, Simmons & Geisler 1998), whereas vision remained important or evolved further in megachiropterans (Simmons & Geisler 1998, see also references herein).

The possibility that bats and dermopterans may be closely related has been discussed many times. Combined morphological and molecular

data support a sister-group relationship between these two groups (Novacek 1994, Simmons 1995). Simmons (1995) listed 17 morphological synapomorphies shared by Chiroptera and Dermoptera (the clade Volitantia), including tooth, cranial, and postcranial characters. Several shared characters are related to gliding/flight performance, such as the presence of a humeropatagialis muscle, which tautens the plagiopatagium during flight, elongated forelimbs with interdigital patagia, increasing the glide surface, and modifications in radius and ulna for stability and restriction of movements. Bats and dermopterans also share some characters in the feet that are adaptations for grasping and underbranch hanging, such as elongated fourth and fifth toes and the tendon locking mechanism permitting hanging without continuous contraction of the flexor muscle of the toes. The bat lineage passed through a gliding stage before powered flight evolved (Norberg, U. M. 1985 & 1986 b). Dermopterans are 'preadapted' for flight in several characters and it is reasonable to believe that the gliding proto-bat was similar to dermopterans in many respects, if not directly related. The various steps in the evolution of powered flight is discussed below.

3. The evolution of flight in bats

3.1. The main theories

There are two major hypotheses on the origin of powered flight in vertebrates, the "trees-down" (or arboreal) theory (Bock 1986, Darwin 1859, Feduccia 1980, Marsh 1880, Norberg, U. M. 1985 & 1986 b) and the "ground-up" (or cursorial) theory (Caple et al. 1983, Nopsca 1907 & 1923, Ostrom 1974 & 1986). The arboreal theory suggests that powered flight in birds, bats, and pterosaurs evolved via *gliding* in tree-living animals, whereas the ground-up theory holds that flapping flight in birds and pterosaurs evolved in ground-running and jumping animals without a gliding intermediate. It has been suggested that proto-bats foraged for insects by jumping from trees or cliffs and that flight evolved from this behaviour (Caple et al. 1983, Jepsen 1970). Caple et al. (1983) further suggested that the proto-bats made ballistic jumps to a lower level, while catching insects.

Norberg, U. M. (1985, 1986 b & 1990) discussed the various theories and concluded that,

from energy- and time-saving arguments as well as for aerodynamic reasons, the gliding theory is a much more feasible hypothesis than the running-jumping-leaping and jumping ones, since in gliding the animal works *with* gravity and not *against* it as in the ground-up theory. The different, hypothetical, steps in the evolution of flight in bats can be sketched as follows.

3.2. Hypothetical steps

Bats may have developed from insectivores or dermopterans that may have been foraging in trees by gleaning insects. At that time they might not have been able to jump after flying insects, which evolved flight long before the bats did and were highly manoeuvrable at the time proto-bats were supposed to have hunted for them. Without good manoeuvrability in the air, jumping proto-bats would have had great difficulties catching flying insects, and if they did manage, they would have got only one insect per jump and had to climb up again before the next attack. Such a foraging would be hopelessly time- and energy-consuming and ecologically impossible. Ballistic jumps to a lower level would require high control of movements and could be performed only by a well developed flier. These power and control arguments identify immense barriers to the evolution of flight in bats from a jumping behaviour without any intermediary gliding stage.

Maximizing net energy gain during foraging in trees or among cliffs might have been a reason for strong selection for increased gliding performance in early bats. Gliding from one tree to another and climbing upwards during foraging is a way to maximize net energy gain by modern birds (Nopsca 1907, Norberg, R. Å. 1977). This behaviour may have been beneficial for the proto-bats as well. Once a glide surface had evolved, the bat's energy and time demands for locomotion might have been drastically reduced and their foraging efficiency would have been increased. The initially small glide surfaces made the first glides steep. But even steep parachuting jumps from trees could have reduced the time and energy required for locomotion during foraging. Larger gliding area decreased gliding speed and allowed safer landings. Gliding in proto-fliers must have been used for transportation and not for insect-catching. Hawking insects in the air requires high manoeuvrability, which could not have appeared until true flight was established.

Steep gliding (parachuting) for escape might also have been important for arboreal animals (Bock 1965 & 1986). Even squirrels without a

glide membrane leap among branches and trees and spread whatever they have (legs, tail) to glide on. This behaviour strongly promotes every incipient skin surface for gliding purposes before a glide area occurs.

The next step is intermittent flapping; the proto-bat began to flap during the gliding. A net thrust force can be produced even during very slight flapping in a gliding animal while maintaining the necessary vertical lift, resulting in a shallower glide path (Norberg, U. M. 1986 b). For every step along the hypothetical route from gliding to powered flight, through stages of incipient flapping, there would have been an advantage over previous stages in terms of control and length of the flight path. Longer wings, more efficient wing profiles, and increased abilities for wing flexion and movement coordination eventually led to horizontal flight.

The selection pressure for good control of movements must have been high in the early gliders; better control would have allowed them to change course to reach a particular destination. Therefore, good stability and control of movements were probably achieved before flapping flight evolved, and may have improved progressively along with the ability to glide. Stability and control of movements can be achieved by simple wing movement coordination, such as twisting, retraction, and control of dihedral angle. Eventually, more sophisticated wing characters evolved and increased the bat's manoeuvrability permitting the bat to hawk insects in the air.

3.3. Ancient bats

The early bats may have used powered flight primarily for transportation between foraging sites (Norberg, U. M. 1986 b). As mentioned above, a certain degree of manoeuvrability was needed before the bats could utilize the air space for foraging. This favoured selection for insect-catching in the air with concomitant increased manoeuvrability. Radiation to different flight habits led to different wing forms specialized for different foraging and flight modes (Norberg, U. M. 1986 b).

Ancient bats had short and rather small wings and they resembled extant frugivorous bats in this respect. Their wingtips were extremely short but slightly rounded, indications of a fairly manoeuvrable flight (Norberg, U. M. 1989, 1994, Norberg & Rayner 1987). Frugivorous and nectarivorous bats still use flight primarily for transportation between roosts and food places, and they are those bats that resemble the ancient bats most in wing design (Norberg, U. M. 1989). The

Table 1. Codes used in diagrams for bat species.

<i>Ap, Azp</i>	<i>Antrozous pallidus</i>
<i>Cag, Cha</i>	<i>Chrotopterus auritus</i>
<i>Cc</i>	<i>Cardioderma cor</i>
<i>Emm</i>	<i>Emballonura monticola</i>
<i>Ems</i>	<i>E. semicaudata</i>
<i>Es</i>	<i>Eptesicus serotinus</i>
<i>Hc</i>	<i>Hipposideros commersoni</i>
<i>Hd</i>	<i>H. diadema</i>
<i>Lab</i>	<i>Lasiurus borealis</i>
<i>Lai</i>	<i>L. cinereus</i>
<i>Ley</i>	<i>Leptonycteris yerbabuenae (sanborni)</i>
<i>Lf</i>	<i>Lavia frons</i>
<i>Lnn</i>	<i>Lasionycteris noctivagans</i>
<i>Mb</i>	<i>Myotis blythi</i>
<i>Mc</i>	<i>Macrotus californicus</i>
<i>Mdg, Mg</i>	<i>Macroderma gigas</i>
<i>Mia</i>	<i>Miniopterus australis</i>
<i>Mii</i>	<i>M. inflatus</i>
<i>Mis</i>	<i>M. schreibersi</i>
<i>Mel, Ml</i>	<i>Megaderma lyra</i>
<i>Mm</i>	<i>Myotis myotis</i>
<i>Ms</i>	<i>Megaderma spasma</i>
<i>Mv</i>	<i>Myotis vivesi</i>
<i>Mya</i>	<i>Myotis albescentis</i>
<i>Myad</i>	<i>M. adversus</i>
<i>Mybo</i>	<i>M. bocagei</i>
<i>Myd</i>	<i>M. dasycneme</i>
<i>Mydb</i>	<i>M. daubentoni</i>
<i>Myg</i>	<i>M. grisescens</i>
<i>Mylu</i>	<i>M. lucifugus</i>
<i>Myv</i>	<i>M. velifer</i>
<i>Myy</i>	<i>M. yumanensis</i>
<i>Na, Noa</i>	<i>Noctilio albiventris</i>
<i>Ner, Nr</i>	<i>Nycticeius rupepelli</i>
<i>Ng</i>	<i>Nycteris grandis</i>
<i>Nl, Nol</i>	<i>Noctilio leporinus</i>
<i>Nyl</i>	<i>Nyctalus leisleri</i>
<i>Oh</i>	<i>Otonycteris hemprichi</i>
<i>Ph</i>	<i>Phyllostomus hastatus</i>
<i>Pip</i>	<i>Pipistrellus pipistrellus</i>
<i>Piu</i>	<i>P. nathusii</i>
<i>Pzv</i>	<i>Pizonyx vivesi</i>
<i>Rh</i>	<i>Rhinolophus hipposideros</i>
<i>Tab</i>	<i>Tadarida brasiliensis</i>
<i>Tc</i>	<i>Trachops cirrhosus</i>
<i>Vem</i>	<i>Vespertilio murinus</i>
<i>Vs</i>	<i>Vampyrus spectrum</i>

wing forms of ancient bats suggest that they foraged or lived among vegetation (Habersetzer & Storch 1987) and may have been perch-hunters (Norberg, U. M. 1989). There is nothing in their wing shapes to indicate that these bats were poor fliers.

4. Flight mechanics and wing design

Some flight mechanics are needed to understand how wing design is related to flight mode, because the optimal wing form of flying animals

Table 2. Flight speeds of bats. Data for wing loading and aspect ratio are taken from Norberg and Rayner (1987). (From Norberg, U. M. 1987).

species	average speed (m/s)	maximum speed (m/s)	wing loading (N/m ²)	aspect ratio	source
open-field flight speeds (filled circles) ¹⁾					
<i>Saccopteryx bilineata</i> (Emballonuridae)	5.5	6.2	5.9	6.1	Morrison (1980)
<i>Lavia frons</i> (Megadermatidae)	6.6		12.0	5.4	Norberg, U. M. (1987)
<i>Noctilio leporinus</i> (Noctilionidae)	8.9		15.2	9.0	Goodwin (1928)
<i>Phyllostomus hastatus</i> (Phyllostomidae)	8.6	12.3	25.2	7.6	Morrison (1980)
<i>Artibeus jamaicensis</i>	8.2	9.0	16.6	6.4	Morrison (1980)
<i>Myotis lucifugus</i> (Vespertilionidae)	5.7	6.9	7.5	6.0	Patterson & Hardin (1969)
<i>M. sodalis</i>	5.6	6.7	6.5	5.4	Patterson & Hardin (1969)
<i>M. velifer</i>	6.3	6.7	5.6	6.2	Twente (1955)
<i>Pipistrellus subflavus</i>	5.2	6.9	5.6	6.2	Patterson & Hardin (1969)
<i>Nyctalus noctula</i>	14.4		16.1	7.4	Kolb (1955)
<i>Eptesicus fuscus</i>	9.3	10.5	8.4	6.4	Patterson & Hardin (1969)
<i>E. serotinus</i>	9.8		12.2	6.5	Lynn Allen (1961)
<i>Miniopterus schreibersi</i>	14.4		10.2	7.0	Constant & Cannonge (1957)
<i>Tadarida pumila</i> (Molossidae)	8.3		10.8	8.4	Norberg, U. M. (1987)
indoor and cave* flight speeds (open circles) ¹⁾					
<i>Eidolon helvum</i> (Pteropodidae)	4.5		30.6	6.9	Kulzer (1957)
<i>Rousettus aegyptiacus</i>	4.4		24.6	5.9	Möhres & Kulzer (1968)
<i>Rhinolophus ferrumequinum</i> (Rhinolophidae)	5.5		12.2	6.1	Kulzer (1968)
<i>Macrotus californicus</i> (Phyllostomidae)	5.1	5.6	10.2	6.4	Hayward & Davies (1964)
<i>Myotis californicus</i> (Vespertilionidae)	3.5	3.8	4.8	5.6	Hayward & Davies (1964)
<i>M. grisescens</i>	5.0*		7.2	6.4	Kennedy & Best (1972)
<i>M. keeni</i>	3.5	4.0	5.9	5.8	Hayward & Davies (1964)
<i>M. lucifugus</i>	3.7	6.1	7.5	6.0	Patterson & Hardin (1969)
<i>M. myotis</i>	4.6		11.2	6.3	Hayward & Davies (1964)
<i>M. sodalis</i>	3.6	5.4	6.5	5.4	Patterson & Hardin (1969)
<i>M. sodalis</i>	4.8*	5.5	6.5	5.4	Patterson & Hardin (1969)
<i>M. thysanodes</i>	3.8	4.4	5.6	6.1	Hayward & Davies (1964)
<i>M. velifer</i>	4.5	5.7	5.6	6.2	Hayward & Davies (1964)
<i>M. volans</i>	4.4	4.7	7.0	5.8	Hayward & Davies (1964)
<i>M. yumanensis</i>	3.6	4.0	7.8	6.3	Hayward & Davies (1964)
<i>Lasionycteris noctivagans</i>	5.0	5.2	7.2	6.6	Hayward & Davies (1964)
<i>Pipistrellus hesperus</i>	2.4	2.7	5.9	5.7	Hayward & Davies (1964)
<i>P. subflavus</i>	3.5	5.4	5.6	6.2	Patterson & Hardin (1969)
<i>Eptesicus fuscus</i>	5.0	6.9	8.4	6.4	Hayward & Davies (1964)
<i>Lasiurus borealis</i>	3.5	6.1	7.4	6.6	Patterson & Hardin (1969)
<i>Lasiurus cinereus</i>	5.1	5.9	10.9	7.7	Hayward & Davies (1964)
<i>Plecotus townsendii</i>	4.1	5.5	6.4	5.9	Hayward & Davies (1964)
<i>Antrozous pallidus</i>	4.0	4.7	7.7	6.7	Hayward & Davies (1964)
<i>Tadarida brasiliensis</i> (Molossidae)	6.0		10.8	8.2	Hayward & Davies (1964)
<i>T. molossa</i>	4.4	5.1	15.4	9.5	Hayward & Davies (1964)
speeds of bats released within vegetation (triangles) ¹⁾					
<i>Pteronotus davyi</i> (Mormoopidae)	4.4		8.0	8.3	Kennedy et al. (1977)
<i>Mormoops megalophylla</i>	5.4	10.2	11.2	7.1	Kennedy et al. (1977)
<i>Myotis velifer</i> (Vespertilionidae)	3.1	3.5	5.6	6.2	Kennedy & Engbretson (1974)
take-off speed (open star) ¹⁾					
<i>Otomops martiensseni</i>	6.6		14.9	9.3	Norberg, U. M. (1987)
before-landing speed (filled star) ¹⁾					
<i>Eidolon helvum</i> (Pteropodidae)	3.8		30.6	6.9	Norberg, U. M. (1987)

¹⁾ see fig. 7

is dictated by mechanical and aerodynamic rules (Norberg, U. M. 1987, 1990, 1995, Norberg & Rayner 1987, Pennycuik 1975 & 1989).

A flying bat must do work with its flight muscles to move the wings in order to generate lift and thrust. The rate at which this work is done is the mechanical power **P** required to fly.

For sustained forward flight the vertical lift **L** must balance body weight **Mg** (body mass times acceleration of gravity), **L = Mg**, and the horizontal thrust **T** produced must balance the overall horizontal drag **D**, **T = D**.

The mechanical power required to fly is the product of thrust and speed **V**, **P = TV = DV**. It