



# FAUNA *of* AUSTRALIA

## 42. VESPERTILIONIDAE

L. S. HALL & D. P. WOODSIDE



## DEFINITION AND GENERAL DESCRIPTION

The Vespertilionidae is the largest family of Australian bats and is one of the most widely dispersed group of mammals in the world. Its members are found throughout Australia and on most off-shore islands (Hall 1981). As might be expected, this large and adaptable group of bats displays a correspondingly diverse range of morphological variation.

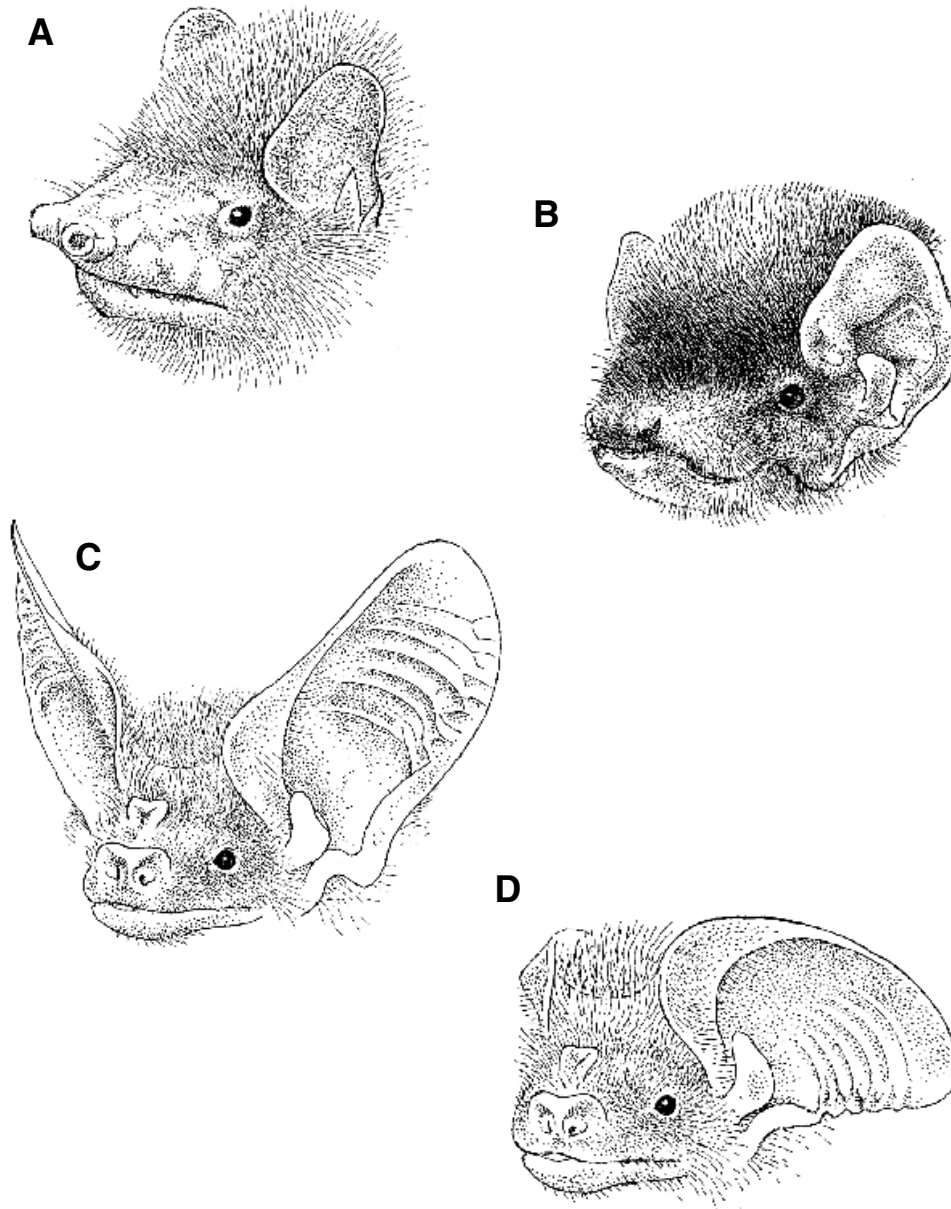
A number of features distinguishes the group as a whole from other Australian bats. Generally, the muzzle is simple, although the Tube-nosed Insectivorous Bat (*Murina florium*; Fig.42.1a) has small tubular nostrils similar to those found in the pteropodid genus *Nyctimene*. The facial region may have a variety of swollen glands and related structures. A true noseleaf is universally absent, but members of the subfamily Nyctophilinae have rudimentary, fleshy nasal flaps (Fig. 42.1b). The eyes are usually small, except in the Nyctophilinae where they are reasonably prominent. The ears of vespertilionids are generally separate, small and simple in structure, but again the Nyctophilinae is an exception as its members have quite long ears (Fig. 42.1c). When at rest or sleeping, members of the Nyctophilinae concertina their ears and cover them with the leading edge of the ear (Fig. 42.1d). When the animals are active, the ears are extended by blood pressure. The tragus is usually a simple tongue-shaped structure, but in the Golden-tipped Bat (*Phoniscus papuensis*) it is long, narrow and pointed. Occasionally, the lower margin of the ear is attached low on the side of the head just behind the corner of the mouth. This is most pronounced in *Chalinolobus*, where the ear connection forms a small fleshy lobe at the angle of the mouth. The tail membrane (uropatagium) is extensive and encloses the tail which extends to its posterior border.

Most vespertilionids are brown, grey or blackish brown in colour. The Pygmy Long-eared Bat (*Nyctophilus walkeri*) has yellowish brown fur and the Little Pied Bat (*Chalinolobus picatus*) and Large Pied Bat (*C. dwyeri*) have black fur with a white strip where the belly fur meets the wing membrane. Frequently almost black fur of the Hoary Bat (*C. nigrogriseus*) has a white frosting. The fur of the Golden-tipped Bat (*C. nigrogriseus*) is long and of a mottled orange and light brown colour. Belly fur is generally lighter than back fur.

Internally, vespertilionids are distinguished by the highly developed double articulation between the scapula and humerus, the very rudimentary ulna, the essentially unmodified shoulder girdle and pelvis and the conspicuous anterior emargination of their bony palate. There is a general trend throughout the family whereby the jaws are shortened to increase the effectiveness of the chewing muscles (Fig. 42.2). This results in a reduction in the number of teeth, which varies from a total of 38 in *Myotis* to 30 in *Nyctophilus*. The ulna is usually fused with the radius at its head and the shaft is reduced to a fine ossified fibrous strand. The third finger bears three phalanges, of which the distal one is cartilaginous throughout except at the extreme base where a distinct joint is formed with the middle phalanx. The seventh cervical vertebra and all lumbar vertebrae are free and there are no postorbital processes on the skull.

The nasal muscle (occipitofrontalis) ends anteriorly in a strong tendon that attaches on the nasal cartilage in the midline of the dorsal side of the nose. As a result of the mobility of the nose and upper lip, the connection between the intermaxillaries is broken and the anterior margin of the nasal bones is forced backward. In all other bats the nasal muscle either ends anteriorly in a fleshy protruberance or is transformed into a thin tendinous sheet spreading over the back or sides of the nose (Winge 1941).





**Figure 42.1** The morphology of the head of three genera of vespertilionids: **A**, Tube-nosed Insectivorous Bat (*Murina florum*); **B**, Gould's Wattled Bat (*Chalinobus gouldii*); **C**, Lesser Long-eared Bat (*Nyctophilus geoffroyi*); **D**, Lesser Long-eared Bat with its ears down. (© ABRS) [F. Knight]

## HISTORY OF DISCOVERY

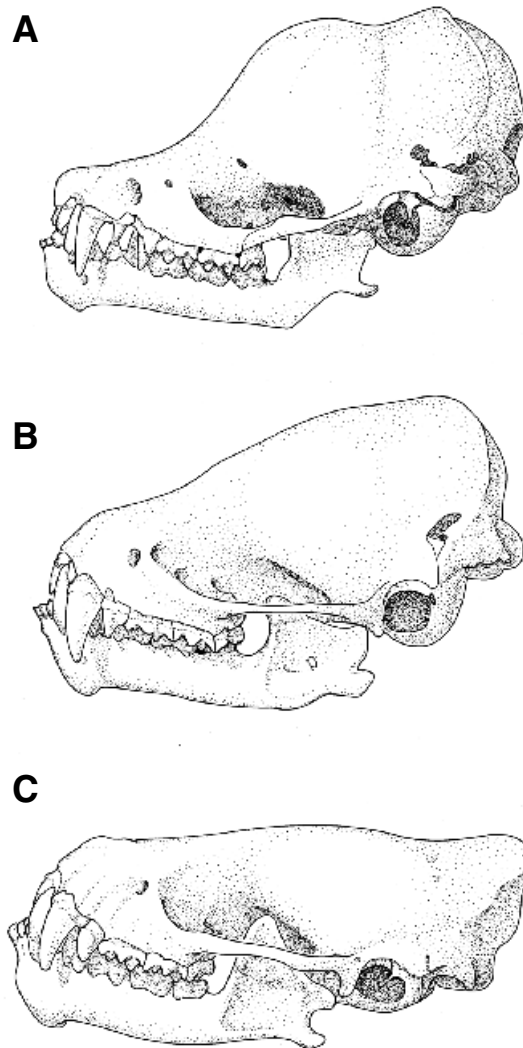
In 1758, Linnaeus recognised seven bats, all of which he placed in *Vespertilio*, the fourth and last genus of the Order Primates. In the first of his many papers on bats, Gray (1821) excluded the flying lemur from the Order and divided the bats into the two main subdivisions which are still in use today. According to Gray there were two suborders, the Fructivorae and Insectivorae, the former containing the families Pteropidae and Cephalotidae, the latter the Noctilionidae and Vespertilionidae. Though Gray's system was not followed very closely during the succeeding fifty years, it was finally given definite form by Gill (1872) and Dobson (1878) and since then has been almost universally adopted.

## MORPHOLOGY AND PHYSIOLOGY

### External Characteristics

Vespertilionids are small microchiropterans, usually with dull brown fur. The smallest species weigh only 3 g while the largest weigh up to 35 g. Females are usually slightly heavier than males.

The face of a vespertilionid is simple and without any prominent noseleaf or disfiguring glandular structures (Fig. 42.1). An exception to this is the small rudimentary noseleaf on *Nyctophilus* (see Churchill, Hall & Helman 1984), the fleshy lobes at the corner of the mouth in *Chalinolobus* and the short tubular nostrils of *Murina*. A tragus is always present in the ear. Most species have short, round, or funnel-shaped ears with the exception of the long ears in *Nyctophilus* which can be concertinaed when not in use. The tail is fully enclosed in an extensive interfemoral membrane and there are no wing or wrist pockets. The thumb is small and all other digits are clawless and enclosed in the wing membrane.



**Figure 42.2** Lateral views of the skulls of: **A**, Common Bent-wing Bat (*Miniopterus schreibersii*); **B**, Gould's Wattled Bat (*Chalinolobus gouldii*); **C**, Little Broad-nosed Bat (*Scotorepens greyii*). (© ABRS) [F. Knight]

### Body Wall

The integument is covered by one of a variety of fur types. The fur is long and thick in *Phoniscus* and is generally short in *Eptesicus* and *Scotorepens*. The wings, tail membrane and ears of *Phoniscus* and *Murina* are covered with sparse, but often long, hair. The dermis is thicker on exposed areas such as the feet and lips and thinnest on the wing and tail membranes. The dermis contains a number of glandular structures. Facial glands are prominent on the muzzle of *Nyctophilus* and *Scotorepens* and, to a lesser extent, on *Eptesicus* and *Chalinolobus*. Labial and circumanal glands have also been recorded (Quay 1970a).

### Skeletal System

No constant readily observable feature distinguishes the vespertilionid skull (Fig. 42.2) can at once be recognised exists. The premaxillaries are present and fused to the surrounding bones. The palate is widely emarginate anteriorly in a broad U between the canines and is extended some distance posteriad of the molars, narrowing abruptly at the last molar and becoming more or less parallel-sided. The dental formula varies considerably, there being totals of 30, 32, 34, 36 or 38 teeth in different genera, an unusually wide range due to variations in number amongst the incisors and premolars. Throughout the family there are three incisors on each side of the lower jaw and normally two in the upper, but the latter are reduced to one in *Scoteanax* and *Scotorepens*. Whatever their number, in the upper jaw the incisors are generally sited close to their respective canines and are always widely separated from those of the other side. The premolars of the upper jaw vary from one to three and those of the lower jaw may be two or three. The combinations of these tooth numbers play a major part in the taxonomy of the family. However, tooth character is not as constant as it was formerly assumed to be, owing to the obsolescence of premolars in genera in which they may normally be thought to be present. In some genera, the molars show a reduction from the customary W-pattern until the posterior tooth in the upper jaw is very short from back to front, little more than half the normal molar remaining.

There are no postorbital processes or enlarged supraorbital ridges, but slight sagittal and supraoccipital crests in some genera are developed into a posteriorly projecting 'helmet'.

The vertebral column of vespertilionids is typically mammalian and usually consists of seven cervical, 11 or 12 thoracic, five lumbar and three to five sacral vertebrae. The number of caudals ranges from none to 12. Fusion occurs at several points and the seventh cervical and first thoracic are usually fused. The axis is the only cervical vertebra to bear a spinous process (Dobson 1878). All the thoracic vertebrae bear ribs, but lack neural spines except in *Miniopterus*, where Barbu (1960) reported rudimentary spines.

The chiropteran sacrum is generally fused and sutures between vertebrae may or may not be evident. The least amount of fusion is seen in vespertilionids (Walton & Walton 1968). The caudal vertebrae are simple, cylindrical bows generally lacking processes and always lacking neural canals. In *Miniopterus*, the second caudal bears a haemal process on the mid-vertebral line, the neural spine on the first caudal is in the form of a crest and the third caudal is larger than the first two (Barbu 1960).

The sternum is composed of the manubrium and the body (mesosternum and xiphoid portions). A characteristic notch is present in the posterior margin on the lateral lobe of the manubrium. The ribs are equal in number to the thoracic vertebrae and are noted for their proportional length.

As in many other families, there is a deep notch in the coracoid border of the scapula in the Vespertilionidae. The axillary border is also notched and a ventrally directed flange from the coracoid border of the scapula in the Vespertilionidae is present (Walton & Walton 1970). The clavicle is very large, quite long and curved and articulates distally with the scapula and proximally with the lateral process of the sternal manubrium. The head of the humerus always projects medially from the long axis of the shaft and is generally circular in outline. The shaft of the radius is generally arched slightly and there is a large processus ulnaris radii in *Miniopterus* (Barbu 1960). A locking mechanism involving the spinous process of the medial epicondyle of the humerus and the proxima-medial part of the radius is present (Vaughan 1959). The locking mechanism at the joint limits lateral movement so that the joint becomes a hinge only for stretching and flexing the forearm.

The ulna is generally considered to be composed of a proximal and distal part. The proximal portion is free at the weak olecranon and this process is continuous with an arched rod-like shaft which unites distally with the radius. Among the vespertilionines, however, the shaft may terminate in the forearm muscle, whereas in *Nyctophilus* and *Chalinolobus* a shaft is entirely absent (Miller 1907). Digits III, IV and V comprise three phalanges. Terminal cartilages have been recorded for many species of bats and Miller (1907) considered that the distal phalanx of digits IV and V is always cartilaginous and the digit V bears with an accessory cartilage which projects from the margin of the wing membrane.

The bones of the pelvic girdle are united ventrally in a symphysis pubis in all mammals. In bats, only males possess a symphysis. The femur is similar in construction to the basic mammalian pattern. In some of the Vespertilionidae the trochanters are drawn backward. Miller (1907) described a complete fibula for the Vespertilionidae. The tarsus is short in bats and is composed of seven bones, the arrangement of which differs little from the typical mammalian pattern. An additional bone, the calcar, is associated with the first row of tarsal bones. It is generally described as a detached portion of the calcaneus (Walton & Walton 1970), but its origin and construction are still in question. The phalangeal formula for the foot is 2-3-3-3-3; there are five toes, all of equal length and possessing a claw. In *Myotis adversus* the toes are elongated and laterally flattened, but in most other vespertilionids the foot is rather unspecialised.

### Locomotion

The most important modifications serving to lighten the wings of bats involve both skeleton and muscle and serve to transfer the burden of controlling the wings from small, distally situated muscles, to large, proximally situated muscles. In general, the mechanical arrangements of the muscles of the forelimb are such that extension of the humerus by the large muscles that power the downstroke causes an automatic extension of the forearm and a spreading of the distal part of the wing. There is a considerable variation in the size of the musculature of the forearm in bats, and the more advanced families, such as the Vespertilionidae, have smaller and lighter forearm musculature.

The members of the Vespertilionidae differ widely in the shapes of their wings and, consequently, in their flight characteristics. Generally, the wings of vespertilionids are moderately long and average about twice the length of the head and body (Smith & Starrett 1979). The greatest winglength occurs in *Miniopterus*, where the wings are nearly 2.5 times longer than the head and body. Due to the morphological diversity of the group, wing aspect ratio (wingspan divided by the mean width of the wing) varies greatly (Smith & Starrett 1979). Dwyer (1965a) recorded the following wing aspect ratios for Australian vespertilionids: Greater Broad-nosed Bat (*Scoteanax rueppelli*) 7.3;

*Scotorepens orion* 7.6; Little Broad-nosed Bat (*S. greyii*) 7.6; Greater Long-eared Bat (*Nyctophilus timoriensis*) 6.5; Lesser Long-eared Bat (*N. geoffroyi*) 6.5; Large-footed Mouse-eared Bat (*Myotis adversus*) 7.5; Common Bent-wing Bat (*Miniopterus schreibersii*) 8.3; Little Bent-wing Bat (*M. australis*) 7.5; Great Pipistrelle (*Falsistrellus tasmaniensis*) 8.9; Little Cave Eptesicus (*Eptesicus pumilus*) 8.9; Gould's Wattled Bat (*Chalinolobus gouldii*) 7.6; and Chocolate Wattled Bat (*C. morio*) 7.2.

In comparison with other families, the vespertilionids have well-developed uropatagia (high values for wing area/uropatagial area) and reduced loading (Dwyer 1965a).

### Feeding and Digestive System

A wide variety of flying and non-flying invertebrates are fed on by bats (Vestjens & Hall 1977). The prominent canines and high cusped tribosphenic molars quickly reduce the tough chitinous insect exoskeleton to small fragments. The tongue, oral cavity and oesophagus of vespertilionids reflect the needs of a small mammalian insectivore. Differences in the shape and relative proportions of gastric glands in the stomach have been shown in non-Australian vespertilionids (Forman 1972). The stomach of vespertilionids is a simple mammalian stomach. There is no detectable oesophageal sphincter; rather, the lower oesophagus enlarges to form a cone, lined with gastric, rather than oesophageal, mucosa.



**Figure 42.3** Vespertilionid techniques for capturing insect prey on the wing.  
(© ABRS) [F. Knight]



### Circulatory System

Bat hearts are large and they include the largest, relative to body weight, found in mammals (Clark 1927). Kallen (1977) stated that bat hearts are strikingly elongate when empty and nearly spherical when full, suggesting that bats have an impressive stroke volume. Although typically mammalian, the heart shows a number of characteristic modifications. A bicuspid valve is present where the inferior vena cava enters the right atrium. The right atrium is often tube-like immediately cranial to this valve, appearing to be an extension of the inferior vena cava itself. In the left atrioventricular valve, in addition to typical chordae tendinae, a discrete flat muscular band extends from each papillary muscle to each valvular commissure.

In the heart of vespertilionids only a vague sinoatrial node is recognisable and ordinary cardiac muscle fibres connect the atria to the ventricles (Martini 1959). The heart rate of those vespertilionids studied varies from a maximum of 900–1300 beats per minute while active or flying, to 400 while resting, and to less than 50 beats per minute for cold hibernating bats (Kallen 1977).

During rest, the body temperature of most vespertilionids is close to the ambient temperature (Kulzer *et al.* 1970). The rewarming speed of vespertilionids is rapid and most appear to be able to undergo some form of torpor. Kulzer *et al.* (1970) also showed that specimens of Large-footed Mouse-eared Bats from Cairns, Queensland could be induced into torpor by lowered temperatures. The animals stayed in deep torpor for 3 weeks and individuals were able to rewarm themselves either spontaneously or after mechanical stimulation. They lost 14–20 mg of body weight each day (Kulzer *et al.* 1970). Morrison (1959) recorded that the Common Bent-wing Bat cannot crawl when its body temperature is less than 22.7°C. Flight first occurs when body temperature reaches 31.7°C and after a long flight body temperature varies from 38.7–41.7°C (Morrison 1959).

### Respiration

The ability to fly, echolocate and to catch insects in the mouth while flying, has posed no special constraints or caused morphological adaptation to the vespertilionid respiratory system. It is typical of a small mammal.

During flight, respiration and wingbeat are linked in a one to one relationship at about 10 per second. Expiration is associated with up-stroke and echolocation calls can be emitted at any stage of the respiratory cycle. In flying bats, echolocation calls are most frequently produced near the beginning or the end of expiration.

Respiration rates are usually over 100 per minute while at rest and can reach over 1000 per minute in prolonged and rapid flight in some species. During periods of torpor, respiration rates drop to 10–15 per minute.

### Excretion

The kidneys are roughly equal in size, with the right being more anteriorly located. Kidney weight appears to be influenced by hibernation in Common Bent-wing Bats (Schimoizumi 1959), but Rosenbaum (1970) considered that the tendency towards lethal dehydrative conditions in this state invalidates the observation. The hilus often protrudes beyond the renal body. The bladder is typically mammalian and is lined with transitional epithelium. The microanatomy of the bat kidney was reviewed by Rosenbaum (1970). The kidneys produce a hypertonic urine. Bats also excrete water via faeces and by pneumocutaneous exchange.

### Sense Organs and Nervous System

The vespertilionid tongue contains taste buds on both circumvallate and fungiform papillae. The eye is typically mammalian in structure and size varies across genera. The eyes tend to be small in species that have well-developed acoustic orientation, such as *Miniopterus*, and larger in species which are known to forage close to, or on, the ground (for example, *Nyctophilus*). Although the small eyes of *Miniopterus* would appear to be of limited use, the long distances travelled by this species when dispersing from maternity roosts suggests that acoustic orientation alone would be insufficient. Smell does not appear to be important, but experiments have shown that vespertilionids are able to locate hidden insects over short distances (Suthers 1970). The vomeronasal gland is not usually found, but has been recorded in *Miniopterus* by Matthes (1934).

The auditory centres of the brain are well developed and the superior and inferior colliculi are generally exposed, the latter being the more massive. The surface of the cerebellum is smooth and the cerebral hemispheres show few gyri and sulci.

A striking feature of the spinal cord of vespertilionids is the large cervical ganglia. The large size of these structures is clearly related to the well-developed upper extremities. In contrast, the lumbar ganglia enlargements are scarcely visible. The spinal cord of the Microchiroptera is one of the shortest of all vertebrates. Another distinctive feature is the entrance of the dorsal root fibres, which enter the spinal cord just either side of the posterior median sulcus in Microchiroptera. In most other mammals they enter dorso-laterally (Quay 1970b).

All vespertilionids are capable of echolocation and for the most part make use of frequencies in the ultrasonic range (above 20 kHz). Aspects of their sound production, hearing and analysis of echoes have been intensively studied elsewhere in the world (Simmons, Fenton & O'Farrell 1979; Fenton 1980; Simmons & Stein 1980; Neuweiler 1984) and these findings are generally applicable to Australian species. A vespertilionid, the Little Brown Bat (*Myotis lucifugus*), was the subject of the pioneering work on the use of ultrasonic signals (Griffin & Galambos 1940, 1941). Since then, each species has been shown to solve problems of echolocation in different ways. They have had to cope with the rapid attenuation of their ultrasonic signals in air; with the continuous re-establishment of their position, relative to that of a moving target; and with the use of echoes to discriminate fine target details such as size, shape and texture. The solutions to these problems are varied and generally reflect the habitat in which the bats must perform their tasks (such as hunting and finding roost sites). They also reflect the foraging strategy used by the species and the nature of its typical prey (Fenton 1974, 1982a, 1982b; Simmons & Stein 1980).

Echolocating bats may be separated into three groups, based on the type of signals they use, although Simmons & Stein (1980) argued that there are five groups. Some use signals that are predominantly constant in frequency (CF bats), others use frequency modulated signals (FM bats) and some use combinations of the two systems (CF/FM bats). To a large extent, these groups also reflect the degree of facial ornamentation of the bats and their tendency to emit sounds through their nose or mouth. The CF bats emit sounds through their nose and have highly ornamented nasal discs to project the signals. In this way, they create complicated radiation patterns used to gain details about target prey. The FM bats are the least ornamented and include the vespertilionids, also named the 'plain faced bats'. These bats typically use FM signals to echolocate and are oral emitters. Notable anomalies in this regard are the members of the genus *Nyctophilus* in Australia and *Antrozous* in North America, all of which have rudimentary noseleaves. As suggested by Sales & Pye (1974) in regard to *Antrozous*, and only recently confirmed with *Nyctophilus* (D.P. Woodside,

K. Taylor, L. Hall & J.D. Pettigrew, unpublished data), these bats are capable of nasal emissions, and even their minor noseleaves may generate a radiation pattern that provides additional acoustic information during echolocation.

The advantages and disadvantages of using FM as opposed to CF or CF/FM signals for echolocation have been discussed by Neuweiler (1984) and Simmons & Stein (1980). They concluded that FM bats have improved range detection—the ability to detect small differences in distance—that aids in the detection of fine physical details of the target, but provides very little information on relative velocity of prey. Vespertilionids, therefore, are well equipped to detect the relative position of their prey in three-dimensional space, to describe its shape, size and possibly its texture and even identify the species, but are not likely to locate or successfully pursue very fast prey. Further, the aerodynamic features of vespertilionid bats indicate that most are slow, manoeuvrable fliers (Norberg 1981). They are capable of foraging in a range of habitats, including relatively cluttered ones, relying on their accurate discrimination of details using echolocation and their acrobatic flight. Flight patterns of several Australian vespertilionids were described by Dwyer (1965a) and O'Neill & Taylor (1986).

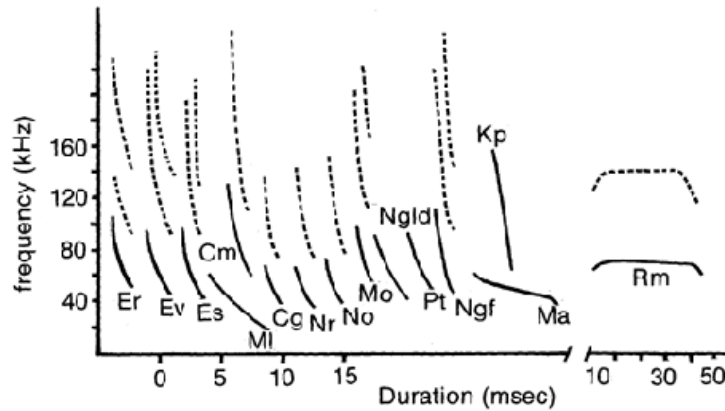
Vespertilionids are reliant on echolocation to navigate and find food. Their vision is less developed than that of some other microchiropterans, such as the Ghost Bat (*Macroderma gigas*) which may make use of sight to hunt, and is poor by comparison to fruit bats (Pettigrew *et al.* 1988). The sense of smell is probably best used to detect social cues at relatively short distances. The ability to listen passively for prey has been demonstrated for *Antrozous* (Bell 1982) and also may be true for *Nyctophilus*, but is likely to be a rare behaviour among vespertilionids. As echolocation is clearly the major 'tool' for habitat exploitation for these bats, it also may be the most important ecological dimension along which coexisting species have become sorted or displaced.

A given bat species may be identified by recording and analysing call sequences (Fenton & Bell 1981). Species censuses (Fenton *et al.* 1976; Woodsworth, Bell & Fenton 1981) and ecological studies can thus be carried out (Fenton & Bell 1979; Fenton *et al.* 1980; Bell 1980b; 1982; Woodsworth *et al.* 1981; Thompson & Fenton 1982) without relying on capture techniques. In Australia, this work has begun only recently (Woodside & Taylor 1985).

The frequencies of calls used by vespertilionids in navigation and detection of prey typically range from 40–100 kHz and are often accompanied by harmonics that serve to broaden the band width of part or all of the call (Fig. 42.4). As shown for some Australian species (Woodside & Taylor 1985), there is some degree of flexibility in the use of harmonics and the duration and fundamental frequencies of the calls used by each species. These dynamic aspects of bat sonar systems are likely to have contributed to the success of the animals in an evolutionary sense.

Not all ultrasonic signals produced by vespertilionids are echolocation calls. Many are social signals and many species have large repertoires of discrete vocalisations (Bradbury 1977b; Fenton 1977; Woodside & Taylor 1985). The idea that echolocation signals may have been derived from one of these social signals is partly substantiated by studies of the ontogeny of echolocation in young vespertilionids (Gould 1971; Kleiman 1969).

Young bats acquire their echolocation skills and social vocal repertoire through practice and mimicry. Emitting only isolation calls at birth, young bats are capable of producing a wide range of social and echolocation signals by the time they make their first forays from the roost 4–5 weeks later. Their early survival is dependent on their skill in echolocation as it is their only means of detecting prey, escaping predators and returning to the safety of the roost.



**Figure 42.4** Frequencies of calls used by various Australian vespertilionid species in navigation and the detection of prey. Dotted line = harmonics; Cg = *Chalinolobus gouldii*; Cm = *C. morio*; Er = *Eptesicus regulus*; Ms = *Miniopterus schreibersii*; Mi = *Mormopterus loriae*; No = *Nycticeius orion*; Nr = *N. rueppellii*; Ngf = *Nyctophilus geoffroyi*; Ngld = *N. gouldii*; Pt = *Pipistrellus tasmaniensis*; Rm = *Rhinolophus megaphylus*. (After Woodside & Taylor 1985)

### Endocrine and Exocrine Systems

Despite the considerable amount of information available on the reproductive biology of Australian vespertilionids, detailed studies on their endocrine organs are few. In all species, the endocrine system is typically mammalian. The paired testes and epididymides lie permanently in the interfemoral membrane and are conspicuously bulbous during the breeding season (Dwyer 1970b; Richardson 1977; Phillips & Inwards 1985). Stages in spermatogenesis are typically mammalian and in the non-active testis the interstitial cells appear to increase, though they contain less cytoplasm than during spermatogenesis (Richardson 1977). Details of the morphology of sperm from eight Australian vespertilionids have been given by Breed & Inns (1985) who considered that variations in acrosome morphology could be used for taxonomic purposes.

The ovaries are spherical, and the left is a little larger than the right. Successive stages of follicle development and atresia are seen in both ovaries at all times of the year in *Miniopterus* (Richardson 1977). Kitchener (1975) recorded polyovular follicles, some with incipient vesicles, in *Chalinolobus*. Detailed measurements of ovaries, follicles and diagrams of the female reproductive tracts were given for Gould's Wattle Bat by Kitchener (1975), for the Chocolate Wattle Bat by Kitchener & Coster (1981) and for the King River *Eptesicus* (*Eptesicus regulus*) by Kitchener & Halse (1978).

Details on other endocrine and all exocrine glands in Australian vespertilionids are lacking.

### Reproduction

The accumulation of reproductive data for the temperate members of this large family is considerable, but the reproductive patterns of tropical vespertilionids are essentially unknown. The King River *Eptesicus* shows a typical vespertilionid pattern with both ovaries being functional, but with implantation restricted to the right horn of the bicornuate uterus (Kitchener & Halse 1978). Typically, spermatozoa are produced during the summer and stored in the



epididymides until spring. Some species copulate during the autumn as individuals gather for periods of torpor and may continue copulating occasionally during winter.

Male Little Forest Eptesicus (*Eptesicus vulturnus*) regularly copulate with dormant females (Tidemann 1982). Spring copulation also occurs in some species that copulate prior to periods of torpor, but most of the individuals involved may be young of that year (Carter 1970).

Ovulation and fertilisation begin at the end of winter and Kitchener (1975) recorded from two to nine ova being shed from each ovary in the polyoestrous Gould's Wattled Bat. Corpora lutea may be deeply embedded in the ovaries and ovulation apparently causes considerable breakdown of capillaries at the point of rupture (Kitchener 1975). Gestation lasts about 3 months. Many Australian vespertilionids are monotocous, but some frequently have two young per pregnancy (for example, Gould's Wattled Bat, Large and Little Pied Bats, Little Cave Eptesicus, Western Broad-nosed Bat (*Scotorepens balstoni*), and the Greater and Lesser Long-eared Bats; Ryan 1963a; Dwyer 1966b, Green 1966; McKean & Hamilton-Smith 1967; Phillips & Inwards 1985). The Large-footed Mouse-eared Bat and the Little Cave Eptesicus are known to be polyoestrous and give birth to young in November/December and again in late January/February (Dwyer 1970b; Maddock & McLeod 1976). Twins have been occasionally recorded in Large-footed Mouse-eared and Chocolate Wattled Bats (Young 1979; Kitchener & Coster 1981). After parturition there is a rapid involution of uterine horns and the vagina, followed by a brief lactational anoestrus. The season of birth varies between and within species. Kitchener (1975) showed that birth dates in Gould's Wattled Bat vary with latitude. Births occur in late November or early December in the south-west of Western Australia and in late September or early October in the northern region of Western Australia.

Detailed studies on the Australian Miniopterinae by Dwyer (1963a, 1966b, 1968), Richardson (1977) and Wallace (1978) gave a clear picture of the reproductive behaviour of these two bats. Both are monoestrous and monotocous; copulation is generally in autumn and parturition occurs in December, but varies somewhat with latitude. The Little Bent-wing Bat copulates during June and July; fertilisation and implantation follow, but development is retarded for about 2.5 months during which time individuals are often torpid. Fertilisation occurs in mid-August and implantation occurs by mid-September. In Common Bent-wing Bats, copulation and fertilisation occur in late May and early June, immediately after a relatively short period of spermatogenesis and about 1 month after the release of sperm to the epididymides. During winter, implantation of the blastocyst stage is delayed. The male accessory glands involute, but a store of epididymal sperm is retained. Implantation occurs in August followed by birth in December.

### Embryology and Development

The gestation period of vespertilionids varies from 2.5–3 months in *Myotis* to around 6 months in *Miniopterus* (Dwyer 1970b; Richardson 1977). Dwyer (1964a) suggested that inhibition of parturition is achieved in *Miniopterus* by the lowering of body temperature by roosting in a cool area of a cave. Within a related group, larger size generally appears to be correlated with a longer period of intrauterine life. All bats are altricial and dependent upon their mother for some weeks after birth. At birth, vespertilionids are essentially naked and blind. The weight of newborn vespertilionids ranges from about 15–30% of the weight of the non-pregnant adult female (Orr 1970) to 35% in the case of twins in Chocolate Wattled Bats (Young 1979). The weight of a newborn *Eptesicus* species was 1.11 g; its mother weighed 3.84 g, according to Green (1965), who

observed contractions at 6 second intervals and a birth process taking about 1 minute. The young had attached to a nipple in the following minute. Breach presentation is a characteristic of vespertilionids (Green 1965, 1966; Carter 1970; Young 1979). Although a few facial vibrissae can be present at birth, body fur does not appear for several days. Newborn young first appear pink, then turn grey as hair follicles and pigment appear. By 2–3 days a light fuzz of hair develops, first on the dorsal areas, then a day or so later on the ventral surface. The eyes of newborn vespertilionids are closed at birth and can take from 1–10 days to open, depending on the species (Orr 1970). The development of the ears parallels that of the eyes. It takes up to 10 days for the ears of some species to become erect.

Newborn bats are capable of slow independent movements. Nodding of the head is common and could indicate a tactile locating system. The thumb and hind feet claws are well developed and are used to grasp their mother's fur. The young of some vespertilionids are capable of flight in 3 weeks (Jones 1967), but most take 5–7 weeks. Dwyer & Harris (1972) have shown that the combination of clustering behaviour and selection of a domed roof allows for the retention of warm air in Common Bent-wing Bat maternity roosts. This elevated temperature has been shown to promote a faster growth rate for young bats (Tuttle 1975).

All vespertilionids have deciduous milk teeth which are highly specialised and assist the young to attach to the maternal teat. The deciduous teeth are curved inwards and have trifid or bifid cusps (Green 1966). The deciduous dentition for most species is I 2/3 C 1/1 PM 2/2 = 22. The permanent canines appear at 3 weeks and the rest are present by 5 weeks. Most young become indistinguishable from adults by the time they are 3–4 months old. Female Gould's Long-eared Bats become sexually active when 7–9 months old (Phillips & Inwards 1985), but most other vespertilionids do not breed until their second year. Male Gould's Long-eared Bats become sexually mature after their first winter, at 12–15 months old (Phillips & Inwards 1985). The first juvenile moult occurs at 15–16 weeks in Large-footed Mouse-eared Bats (Dwyer 1970b).

## NATURAL HISTORY

### Life History

Many aspects of life history are common to all vespertilionids and there are no known aspects unique to the Australian forms. Typically, vespertilionids have one young per year (Carter 1970) although exceptions exist for some Australian species of *Chalinolobus* (Johnson 1964; Dwyer 1966b; Kitchener 1975; Young 1979), *Nyctophilus* (Ryan 1963a; McKean & Hall 1964; Green 1966; Phillips & Inwards 1985) and occasionally for *Eptesicus* (McKean & Hamilton-Smith 1967; Maddock & McLeod 1974, 1976). Most species are monoestrus; exceptions are *Myotis* in Queensland (Dwyer 1970b) and Little Cave *Eptesicus* in Western Australia (Maddock & McLeod 1976). Mating occurs in autumn in the temperate zones or approximately 6 months post-parturition elsewhere in their range. By this time, the young of that year have become independent and may themselves be reproductive, although males most commonly gain reproductive status in their second year (Tuttle & Stevenson 1982).

In readiness for mating, testes descend into the scrotum, becoming enlarged and reddened. The males of some species produce a strong musky odour and oily secretions can be found around the anus or exuding from facial glands situated on the muzzle.

After mating, the onset of gestation may be delayed by any one of three ways. These include: delayed fertilisation through storage of sperm as in *Eptesicus* (Tidemann 1982); delayed implantation of the fertilised egg; or delayed development of the implanted blastocyst as in *Miniopterus* (Richardson 1977; Wallace 1978).

Full onset of gestation generally occurs in the spring and lasts for about 6 weeks, although observations indicate that in Gould's Long-eared Bat (*Nyctophilus gouldi*) gestation apparently can be protracted at any stage of development, subject to inclement conditions. In general, vespertilionids show a great deal of plasticity in their reproductive behaviours, a feature which enables them to adapt to rapid changes in temperature and food availability (Tuttle & Stevenson 1982).

When the young are born, they are completely dependent on their mother. They are hairless, blind and have closed ear canals. They are capable of suckling, gripping the teat with their milk teeth and 'bleating' for their mother's attention. By 1 week of age, their eyes and ears are open, fur covers most of their body and they are probably self-thermoregulating. The rate of development of young, the order of developmental events and the degree of dependency on the mother may vary with the species, latitude, roost selection and the tendency of the species to form large nursery aggregations (Dwyer 1971). In some species, such as Common Bent-wing Bats, the young are attended in large creches (Dwyer 1966b) which are probably re-sorted when the adults return from feeding. Individual recognition of mother and young using odour and acoustic cues does occur in other vespertilionids.

Young begin to test their wings inside the roost at about 3 weeks. They stretch and flap while clinging to the walls of the roost, but should they let go, are capable only of gliding downward. Mortality due to falls from roost walls can be quite high (Dwyer 1966a). By 4–5 weeks, most young can gain altitude in flight, but have not acquired the skills needed to manoeuvre or land. These may not be tested until the young bats begin leaving the roost on short forays, returning to the roost to suckle. At this stage, survivorship is low as many poor fliers or poor echolocators fall prey to other bats or owls or fail to relocate their roost.

There are relatively few estimates of mortality of vespertilionids at different ages and most of these were summarised by Tuttle & Stevenson (1982). They pointed out that survivorship varies with species, season and sometimes sex; any estimates, therefore, should be applied cautiously to general statements about bats. In the case of Red Bats (*Lasiurus borealis*), prenatal mortality may be greater than 8%, mortality to weaning may be 25%, while mortality in the first week of life for South-eastern Myotis (*Myotis austroriparius*) may be as high as 75% (Foster, Humphrey & Humphrey 1978). Survival of volant youngsters in their first year may be only 30%, improving to anything up to 80% as adults (Hill & Smith 1984).

Factors affecting the life history patterns of vespertilionids include:

- the typical size of maternity colonies and their species-specific needs for maternity roosts, whether in a cave or hollow limb of a tree. This will determine whether there should be seasonal migrations to new, distant sites or a local resorting of sex and age classes between roosts in a smaller area of forest;

- non-breeding roost requirements. The availability of suitable roosts and their physical capacity can set limits on the number and dispersion of roosting bats, the resulting social organisation and foraging behaviour of the group (Kunz 1982);

- the thermoregulatory requirements of the species at a given latitude and the need to seek out suitable roost sites (Dwyer 1971);

the presence and duration of periods of torpor to overcome inclement conditions and thereby improve both seasonal survival and longevity;

the tendency to experience parasite loads which may affect age specific survivorship or require shifting roost sites regularly (Kruttsch 1955a; Stebbings 1966).

predation pressure. The main predators in Australia are snakes (Dwyer 1966a), phascogales, rats, dingoes, foxes (Dwyer 1964b), other bats, owls and some frogs (L.S. Hall unpublished; G. Simmons personal communication). Any or several of these predators may lie in wait at the entrance to a colony of bats to catch them as they exit *en masse* through a small space. Some roosts, especially caves, may have been used by bats for thousands of years and, thus, become a dependable resource leading to set behaviour patterns for local predators.

### Ecology

Nearly all vespertilionids are predators of nocturnal invertebrates and feed primarily on flying insects (Vestjens & Hall 1977). Most vespertilionids acquire their food in the air, but some, such as the nyctophilines, are known to glean insects from vegetation and land on the ground when catching prey. The Large-footed Mouse-eared Bat has been recorded raking the surface of water with its hind feet (Dwyer 1970a), presumably for food, as Robson (1984) found fish scales in their faeces. Aerial prey is caught in the tail or wing membrane and transferred to the mouth while in flight (Fig. 42.3). Insects occasionally are caught directly in the mouth.

Differences between species, especially those sharing the same habitat and food resources, can be found in aspects of their foraging behaviours (Fenton & Bell 1979; Barclay 1985a; O'Neill & Taylor 1986), selection of their hunting grounds (Fenton 1982b) or roosts (Kunz 1982), time of emergence and feeding (Kunz 1973) or vertical stratification within a habitat (McKenzie & Rolfe 1986; Taylor & O'Neill 1986). These differences are reflected in the tools they use to exploit their resources, in their echolocation behaviours (Fenton 1984; Neuweiler 1984) and their flight styles and manoeuvrability (Dwyer 1965a; Norberg 1981).

Evidence for resource partitioning is scarce and probably does not exist (Fenton & Morris 1976; Fenton 1980). Herd & Fenton (1983), however, did provide at least some evidence of behavioural displacement of one species by another in areas of overlap. Resource partitioning is often assumed on the basis of studies into the diets of each species in an assemblage. Many bats specialise in certain prey taxa (Ross 1967; Black 1974; Belwood & Fenton 1976; Belwood & Fullard 1984) or prey size (Belwood & Fullard 1984), while other bats (or the same bats at other times) are opportunistic (Fenton & Morris 1976; Anthony & Kunz 1977; Bell 1980b). In Australia, there are very few specialist feeders among the vespertilionids. Robson (1984) showed that Large-footed Mouse-eared Bats tend toward a fish eating diet and D.P. Woodside, K.J. Hews-Taylor & S.K. Churchill (unpublished observation) noted that the Golden-tipped Bat specialises in orb-weaving spiders.

An understanding of the time budget of a bat is a prerequisite for assessing the importance of foraging behaviours and food selection in determining community structure (see Strong *et al.* 1984). It is possible that some vespertilionids spend very little time actually foraging. As a result, the activities that fill the remainder of their time may be more relevant than foraging when determining the differences that enable species to coexist. For example, the partitioning of roost sites among species may be more important. In some cases, each species within a roost site may be found in a predictable location, probably



selected because the site has suitable temperature and light levels or meets social criteria (Kunz 1982). Various bat species may be sorted spatially through overt behavioural interactions or by the use of secondary cues such as odour. These aspects have not been studied in Australia.

In Australia, caves are limited in number and size (with a couple of notable exceptions in the Nullarbor) and, consequently, most of the vespertilionids are forest dwellers. Their roost sites are limited to hollow limbs of trees, forest rubble, loose bark or crevices among rocks. Opportunities for establishing large social or mixed species colonies are dependent as much on the availability of hollow trees, and thus the age structure of the forest, as they are dependent on the gregariousness of the species.

The tendency for Australian sclerophyll forests to burn with some regularity or for forestry authorities to clearfell large patches of vegetation with a subsequent loss of a variety of roost sites, requires that forest-dwelling species either be more aware of alternative roosts or less selective in the nature of the roost. These dynamic and unpredictable features of forest habitats would be reflected in the type of social organisation of the species, colony size and tendency to migrate. Whereas a cave-dwelling bat can rely on the location and conditions of a roost site, given the season, and, therefore, can 'afford' to migrate regularly, a forest-dwelling bat endures a more changeable environment and is less likely to make regular, long distance forays. Rather, a high degree of home site fidelity in the short term, with regular surveillance of nearby habitats is to be expected. This hypothesis has not been tested, but is partly supported by unpublished findings of several field researchers (D.P. Woodside, D. Lunney, C.R. Tidemann, C.R. Williams). The influence of predation pressure or parasite cycles on the dynamics of Australian cave- or forest-dwelling bats has not been studied adequately, but Marshall (1982) provided a lengthy review of bat ectoparasites and host-parasite relationships elsewhere.

### Behaviour

Knowledge of the behaviour of vespertilionid bats in Australia is limited to detailed studies of the cave-dwelling Little and Common Bent-wing Bats. These are the only species for which we have information on the dynamics of natural colonies, migration patterns, population boundaries, mortality patterns, seasonal changes in individual condition and behaviour (Dwyer 1963a, 1963b, 1964a, 1966a, 1966b, 1968, 1969), as well as the ways in which these bats modify their environments (Dwyer 1965a, 1965b). Information on intraspecific vespertilionid behaviour from these and many unpublished studies in Australia together with research conducted elsewhere can be loosely divided into four categories, discussed below. Interspecific behaviour has not been studied in Australia.

Vespertilionids generally exhibit sexual dimorphism, particularly in relation to size, a relevant factor in the interpretation of mating behaviour. Males are usually smaller (Goodwin & Greenhall 1961; Barbour & Davis 1969; Bradbury 1977b) and may be conspicuously so from birth. Differences may occur in mating activity, especially in the use of certain vocalisations, tactile signals, glandular development and secretions (see Bradbury 1977b for discussion).

Sexual displays are not well known. Nothing is recorded to rival the spectacular vocal displays produced by some fruit bats, such as *Hipsignathus monstrosus*, when males are actively forming mating leks (Bradbury 1977a). Instead, as in Townsend's Big-eared Bat (*Plecotus townsendii*), the displays may consist of quiet 'twittering' by the males followed by the rubbing of head glands over the female and finally copulation (Pearson, Koford & Pearson 1952). Some males may be even more passive and may simply position themselves in the roost waiting for the females to gather in harems. Such behaviour has been observed in Large-footed Mouse-eared Bats in Queensland (Dwyer 1970b).

Glandular development and secretions probably play an important role in signalling the sexual status of individuals. In Large Pied Bats, the head and muzzle glands become active in both sexes at the time of breeding (Dwyer 1966c). Throat (gular) glands may develop during breeding in *Nycticeius* and anal glands become active in *Pipistrellus* and *Myotis* (Quay 1970a). Captive Gould's Long-eared Bats show sexual differences in both the seasonality and the colour of secretions from facial glands (D.P. Woodside personal observation). Obvious glandular secretions appear during autumn mating in males and during spring parturition in females. The functional significance of these secretions is clearly different for each sex, although the nature of the information (for example individual marking) may be the same.

As with most microchiropterans, vespertilionids are viewed as socially conservative (Dwyer 1970b). Some species may be solitary, as suggested for the Greater Long-eared Bat (Richards 1983c) and perhaps the Greater Broad-nosed Bat, or they may live in aggregations of 100 000 or more, as in *Minioterus schreibersii oceanensis*.

Social aggregations may exist for many reasons and may be dynamic, changing with reproductive condition, age of the animals or with season. Aggregations may consist of mothers and their young, sex and age classes or individuals gathered for the thermoregulatory advantages of clustering (Dwyer & Harris 1972; Funakoshi & Uchida 1978). In aggregations of any size, a repertoire of social behaviours is required. These behaviours may involve ear biting (see Dwyer 1970b regarding Large-footed Broad-eared Bats), wing flapping, teeth baring or use of a vocalisation called an 'intimidation buzz' (see Orr 1954 regarding *Antrozous pallidus*; Bradbury 1977b for general discussion). Some species of *Myotis* use several vocalisations that are unrelated to echolocation (Fenton 1977) and use of playback experiments has enabled interpretation of their social significance (Fenton *et al.* 1976).

Most of the social vocalisations involve frequencies lower than those used by the same bat during echolocation and show greater variability in duration (Fenton 1977). During flight, some vespertilionids, notably the Lesser Long-eared Bat emit occasional 'honks', presumably to declare their presence to other bats and thereby lay claim to a feeding space or avoid collision. Vocalisations may be used to encourage contact. *Antrozous pallidus* and *Eptesicus fuscus* have been heard emitting a 'purring' sound when in contact with conspecifics (see Orr 1954; Walker 1964, respectively).

A strong bond between mother and young is established shortly after birth and persists beyond the onset of flight and independent foraging. From birth, the young solicit attention by continuously emitting 'isolation calls' now described for many species (Gould 1971; Kleiman 1969), that result in the return of the mother to the roost and a subsequent search for the correct young. Identification may involve both olfactory (Davis, Barbour & Hassell 1968) and acoustic cues, the latter having been most elegantly demonstrated for the molossid bat, Brazilian Free-tailed Bat, *Tadarida brasiliensis* (Gelfaud & McCracken 1986).

Acoustic cues also may be very important for the individual identification of young Gould's Long-eared Bats. Captive mothers continue to find their own offspring in experiments designed to deceive them, including moving young to a location in the roost different from where they were left by their mothers and simultaneously separating twins. Nor did mothers make the wrong choice when young were painted with urine and facial gland secretions of another female (D.P. Woodside unpublished observation). Gustin & McCracken (1986) showed that lactating females of Brazilian Free-tailed Bats are able to distinguish their own facial gland odour from the odour of other lactating females.

From 5–8 days of age, Gould's Long-eared Bats usually cease their isolation calls and begin to respond to the 'twitter' calls made by their mothers as they enter the roost. Successful retrieval of the young follows a well-synchronised duet with the mother; a sequence is repeated when retrieving each twin. This sequence is perhaps similar to the antiphonal exchanges described by Gould (1971) in *Myotis* and *Eptesicus*. The duet and retrieval is then followed by an intense session of grooming and muzzling which presumably marks the young with odorous secretions from the mother's facial gland. These secretions, which are copious and bright orange or yellow, become obvious just prior to parturition and continue at least throughout the two weeks of lactation.

The strong bond between mother and young persists through the critical period when the young are learning to fly. At this stage, the young may emerge with their mothers on short forays during which time they may attempt to mimic her flight patterns and echolocation calls. Later, the young emerge in the company and safety of many other young bats. At this stage, they are easily caught in traps, as they are attracted to the calls of any bat which is already captive.

Direct observations of eight Tasmanian vespertilionid species in four different habitats showed that flight patterns can be categorised into four groups when described in terms of manoeuvrability, speed and proximity to vegetation (O'Neill & Taylor 1986). These categories generally coincided with predictions based on wing shape (Dwyer 1965a) and suggested that a number of different foraging strategies can be used in the same habitat.

Fenton (1982b) described different usages of habitat by an assemblage of bats in northern Queensland, and Thompson & Fenton (1982) provided more detailed observations of the foraging behaviour of Large-footed Mouse-eared Bats. The 'fishing' behaviour of this species, involving the raking of the water surface with its notably large feet (for which it is commonly named), was described by Dwyer (1970a).

Indirect evidence suggests that the largest of Australia's vespertilionids, the Greater Broad-nosed Bat, has a propensity to capture and consume vertebrate prey, including other bats (Woodside & Long 1984). This may reflect a preference for a certain size of prey, regardless of type, and may be a common phenomenon among larger species.

### Economic Significance

The occurrence of vespertilionids in virtually all Australian habitat types is an important consideration in planning large-scale control or conservation programs. The methods used in both control and conservation would have to be exceptionally diverse. The diversity of habitats occupied and the range of most species, however, provide insurance against natural or anthropogenic catastrophes, should they strike any one habitat or region.

The relatively large numbers of vespertilionid bats (tens of thousands may live in one cave), as compared to other mammalian fauna in a given area, means that they contribute substantially to the biomass and are thus ecologically significant. They play a major role as the only truly nocturnal predator of night flying insects. Some of their invertebrate prey are pests of humans and their crops. In Israel, the poisoning of caves, and thus the eradication of insectivorous bats, has been correlated with an unprecedented increase in numbers of noctuid moths which are serious pests of Israeli food crops (Makin & Mendelssohn 1985).

Vespertilionids have the ability to consume up to 25% of their body weight (species range in weight from 3–25 g) in each meal and they may eat two or three meals each night. Even conservative estimates indicate that the quantity of insects taken by a large colony of bats is vast.

Several species have adapted to life in human dwellings or other man-made structures. While this behaviour has led to bats becoming a nuisance in some homes, it also has meant that they have significant impact on the urban insect fauna. The secretive nature of vespertilionids and their propensity for small, dark crevices means that they are rarely noticed and, therefore, are unappreciated. In the same way, they would be difficult to eradicate should it become necessary. Such a situation could arise if a disease such as rabies became a threat and colonial vespertilionids were implicated as vectors.

The study of the transmission of diseases such as rabies or histoplasmosis has been aided by the use of bats, as have several other fields of medical research (see Constantine 1970 for review). Bats have proved to be excellent subjects for the study of tissue repair, due to the transparent nature of their wing membranes. Other work has been done on the maintenance of an embryo during delayed implantation, delayed foetal development and storage of sperm for long periods, all of which are reproductive patterns exhibited by vespertilionid bats. Results of research involving bat ultrasonic sonar systems have led to major developments in guides for the blind (Griffin 1958; Kay 1980) and improved techniques of non-destructive testing of metals by ultrasound (CSIRO 1983).

Bat guano, a rich source of nitrates, occurs in such large deposits in some caves that it has been commercially mined for long periods (see Dwyer & Hamilton-Smith 1965). Large deposits near Rockhampton, Queensland, were used to manufacture gunpowder in World War II. The use of congregations of bats as tourist attractions is under-developed in Australia. Near Rockhampton, Queensland, however, trips to watch the emergence of 100 000 Little Bent-wing Bats from a maternity cave have become very popular.

Efforts should be made to reduce the pressures that already exist on most bat habitats and/or roost sites. The conservation of vespertilionids should focus on a number of important life history characteristics which makes them vulnerable to human disturbances.

Vespertilionids usually mate and give birth in maternity roosts to only one young annually. Disturbance during any part of this process will lead to reproductive failure.

Roost sites generally are selected on the basis of suitable light levels and microclimate (see Hall 1982b, 1982c). Bats will vacate a roost which becomes unsuitable.

Roost selection may vary with season, reproductive status and sex of the animal (see Dwyer 1966b).

The migration of some vespertilionids over large distances to each of their roost sites requires knowledge of the correct location and shortest routes. Such information may be imparted by the older members of a group; the latter, therefore, may be critical to the survival of a colony.

Most vespertilionids are long-lived (perhaps 20 years or more) and are reproductive for many years (one banded *Miniopterus* was known to be reproducing at 18 years of age), but survivorship of the young is very low. Turnover of resident adults, therefore, may be very low and thus in some instances enhancement of juvenile survivorship may be a critical conservation measure.

All vespertilionids spend a long period grooming each day and any poisons contacted by their fur or wings will be ingested. Insectivorous bats are also highly susceptible to insecticides (Clarke, Kunz & Kaiser 1978). Conservation measures should encourage the reduction of the use of harmful chemicals.



The methods available for the capture, tracking or censusing of these bats are limited and dependent on the desired result. Live capture may involve the use of harp traps (Tuttle 1974; Tidemann & Woodside 1978), trip lines (Parnaby 1976) or mist nets, all of which require careful site selection and some prior knowledge of bat behaviour. Because bats learn very quickly and from each other's mistakes, no trap method can be used for prolonged periods in any one location. There are species biases with each of these methods which are best overcome by use of ultrasonic sensing equipment (see Fenton & Bell 1979; Woodside & Taylor 1985).

The capture or banding (see Barclay 1985b for review of techniques) of any vespertilionid requires an appropriate authorisation or licence, as bats are protected fauna in all parts of Australia. Four species may be considered rare or endangered: the Tube-nosed Insectivorous Bat, Golden-tipped Bats, Large Pied Bats and Pygmy Long-eared Bats. By virtue of their roost preferences, a further four species, the Large-footed Mouse-eared Bat, the Common, and Little Bent-wing Bats and the Yellow-lipped Eptesicus (*Eptesicus douglasorum*), come into conflict with human activities and may be considered vulnerable. The maternity site of the Common Bent-wing Bat at Mt Etna is endangered by mining and many colonies in New South Wales and Western Australia are in jeopardy as a result of roost disturbance or habitat destruction around the caves (see Gates *et al.* 1984 regarding bats elsewhere). The woodchipping industries of East Gippsland, Victoria and parts of New South Wales have placed large tracts of the habitat of about 20 species of forest bats at risk (Hamilton-Smith 1978).

## BIOGEOGRAPHY AND PHYLOGENY

### Distribution

The Vespertilionidae has the widest distribution of any Australian bat family. Members of the family are found in every habitat, from the tropical woodlands of the Northern Territory, the deserts of the interior, through the forests of south-eastern and south-western Australia, to the cool temperate rain-drenched forests of south-western Tasmania.

There seems to be no ecological limit to the distribution of the Vespertilionidae (see Koopman 1970; Hill & Smith 1984). One or more members of the family are found on every continent except Antarctica. Two vespertilionid species hold the northern and southern latitudinal records for bat distribution (Koopman 1970, 1982). Various species are also widely distributed on the islands of the Pacific and Indian Oceans.

Several Australian species are noteworthy for their wide distributions. Gould's Wattled Bat has a distribution that includes the whole of continental Australia and Tasmania except Cape York and a small region near the Gulf of Carpentaria. Lesser Long-eared Bats are also found Australia-wide except for Cape York and the rainforest areas south along the eastern mainland coast to about Lismore. Two species of *Scotorepens*, two species of *Miniopterus*, the Little and Western Broad-nosed Bats, and the Common and Little Bent-wing Bats also have exceptionally wide distributions. Apart from the few exceptions noted above, however, the majority of Australia's vespertilionid species have rather restricted distributions.

Several members of the Vespertilionidae may be considered to have an Australian-centred distribution. Their greatest taxonomic diversity occurs within Australia, and diversity decreasing away from Australia into extralimital populations. These species and their distributions are listed in Table 42.1. Hall

(1981) suggested that the major factors influencing bat distribution are availability of food, availability of roost sites and physiological tolerance of local conditions.

**Table 42.1** Details of the extralimital distribution of genera with Australian-centred distributions. With the exception of *Nyctophilus howensis* (known only from subfossil remains), all listed species are extant.

SPECIES	GEOGRAPHICAL REGION	REFERENCE
<i>Nyctophilus microdon</i>	New Guinea	Koopman 1982
<i>Nyctophilus microtis</i>	New Guinea	Koopman 1982
<i>Nyctophilus bifax</i>	New Guinea	Koopman 1982
<i>Nyctophilus howensis</i>	Lord Howe Is.	McKean 1975
<i>Nyctophilus timoriensis</i>	New Guinea	Hill & Pratt 1981
<i>Nyctophilus</i> sp.	New Caledonia	Tate 1942
<i>Nyctophilus</i> sp.	Fiji Is.	Tate 1942
<i>Chalinolobus gouldii</i>	Norfolk Is.	Troughton 1922
<i>Chalinolobus tuberculatus</i>	New Zealand	Daniel & Williams 1981
<i>Chalinolobus neocaledonicus</i>	New Caledonia	Sanborn & Nicholson 1950
<i>Chalinolobus nigrogriseus</i>	New Guinea	Van Deusen & Koopman 1971
<i>Eptesicus pumilus</i>	Lord Howe Is.	Troughton 1920

Various numerical studies have been made of the relationships between the underlying bioclimatic factors mentioned by Hall (1981) and the distribution of certain Australian vertebrate groups (see Nix 1982; Cogger & Heatwole 1984; Pianka & Schall 1984; Braithwaite *et al.* 1985; Longmore 1986). Only two of these accounts gave any consideration to bats. Vespertilionids, however, have not been treated as a separate group in either study and it is not possible, therefore, at this time to draw any conclusions about the actual bioclimatic factors influencing distribution and diversity in this group.

### Affinities with other Groups

In 1892, Winge (cited in Miller 1907) proposed that the Vespertilionidae was allied to the Molossidae and the Natalidae. Miller (1907) extended this group of associated families, based largely on the morphology of the proximal end of the humerus. This led him to suggest that the Natalidae, Furipteridae, and Myzopodidae were related to more derived forms as the Vespertilionidae, Mystacinidae (= Mystacopidae) and the Molossidae. This arrangement is still followed by contemporary authorities, such as Koopman (1970), Smith (1976) and Hill & Smith (1984). Tate (1942) argued that the Vespertilionidae, Thyropteridae, Furipteridae and Natalidae had a common ancestor from which they have diverged steadily. He also suggested that the Thyropteridae lies closest to the Vespertilionidae via a slight resemblance to the Kerivoulinae.

In a family-level phylogenetic analysis of the Order Chiroptera, Van Valen (1979) proposed that the Molossidae and Mystacinidae are sister groups that share a common ancestor with the Vespertilionidae. His infraorder Vespertilionia includes the Molossidae, Mystacinidae, Vespertilionidae and Natalidae, with the latter family including the Kerivoulinae, Myzopodidae, Thyropteridae and Furipteridae. Although Van Valen's views on the scope of the family Natalidae have not been adopted by recent authorities (see, for example, Hill & Smith 1984; Koopman 1984a), those concerning affinities within the group do not represent a radical departure from the opinions expressed by Miller

(1907) and Tate (1942). The consensus view, therefore, is that the Vespertilionidae is closest to the Thyropteridae, Furipteridae and Natalidae on one hand and to the Molossidae on the other.

In Australia, where only the family Vespertilionidae is present, the degree of adaptive radiation varies considerably between genera. Divergence has been moderate to high in *Chalinolobus*, *Eptesicus*, *Scotorepens* and *Nyctophilus* (that is, the regionally unique genera) and low to very low in *Miniopterus*, *Murina*, *Pipistrellus*, *Kerivoula* (*Phoniscus*), *Falsistrellus* and *Scoteanax* (although these last two genera are regionally unique).

With the exception of the endemic *Falsistrellus* and *Scoteanax*, those genera with low to very low divergence are all restricted to tropical and/or mesic habitats. Their low diversity in Australia may be more a reflection of a response to developing aridity throughout the Tertiary (Kemp 1984) than an indication of late invasion from the north. Nowhere throughout their extensive ranges have such specialised genera as *Murina* or *Kerivoula* penetrated arid habitats. This point was not considered by Koopman (1984a).

Most vespertilionid genera present in Australia have inferred northern affinities, although the phylogenetic relationships have not been determined for the majority of genera. Some rather weak inferences have been made about southern affinities for such genera as *Chalinolobus*, *Nyctophilus* and *Eptesicus*. Again, it must be noted that the phylogenetic relationships of these genera are far from resolved. No substantial progress can be made in the area of historical zoogeography until the phylogenetic analyses are complete (Nelson & Platnick 1981).

The two competing sets of hypotheses impinging on any discussion about the origins and evolution of Australia's vespertilionid fauna are: (a) those favouring an all northern invasion and (b) those conceding at least some southern (Gondwanan) affinities. The earliest explicit proponents of the former view were Tate (1946) and Simpson (1961). Tate's view was that invasion, adaptive radiation and counter-invasion (from Australia towards Asia) proceeded throughout the Tertiary. Simpson was more explicit in his comments. He argued for a probable initial invasion in the early Tertiary, followed by adaptive radiation and very little counter-invasion. He also stated that New Guinea has been a major centre for adaptive radiation in the region. He concluded that, as a whole, the Australian bat fauna is only a 'moderately attenuated' sample of the south-east Asian fauna. The views of Tate and Simpson are supported by a reappraisal of Tate's distributional data by Holloway & Jardine (1968).

The arguments put forward by Tate (1946), Simpson (1961) and Holloway & Jardine (1968) are still given great credence. Their arguments and methodology, however, can be criticised on at least two levels. Firstly, their phylogenetic analyses are now either suspect or were clearly superficial (see, for example, discussion of the affinities of Australian *Eptesicus* and *Chalinolobus* presented below). Second, they based their zoogeography on a 'stable earth'. Only recently has the fact of continental drift or plate tectonics entered the debate about the origins and affinities of Australia's bat fauna (Hamilton-Smith 1975; Hand 1984b; Koopman 1984a).

Herskovitz (1972) suggested that the Order Chiroptera may have originated in the Southern Hemisphere. He based his argument on the fact that of all continents, South America has the highest degree of chiropteran endemism. The degree of morphological divergence or level of taxonomic diversity cannot, by itself, constitute sufficient evidence to support his proposition. Hand (1984b) presented a discussion of alternative explanations for the diversity of South America's bat fauna.

Keast (1972a) was inclined to follow Tate and Simpson, largely it seems, because of the apparently ‘depauperate’ nature of the Australian bat fauna, that is, the low level of supraspecific endemism as well as the low species diversity. Keast presented simple numerical analyses to substantiate his views. The intercontinental comparisons of Keast (1972b) could be revised productively when the taxonomic and systematic reviews of Australian bat genera currently in progress have been completed.

Future discussions in this area must acknowledge that plate tectonics sets the time frame for the origins and evolution of Australian bats. In summary:

Africa separated from Gondwana about 90 mybp (Archer 1984), thus setting a very early cutoff point for the easy interchange between the bat faunas of Africa and the remaining Gondwanan elements of Australia, Antarctica and South America;

Australia broke away from Gondwana about 45 mybp (Archer 1984). This sets the latest date for interchange with South America. Some authorities have argued that this early date would have precluded the entry of bats into Australia. Recent evidence from microcomplement fixation studies (Pierson *et al.* 1982), however, has aligned the endemic New Zealand *Mystacinidae* with the *Phyllostomoids* of South America. Since New Zealand rifted from Gondwana about 80 mybp, this would seem to throw open the question of bat dispersal to and from Australia in the Eocene when Australia rifted from Antarctica;

South America remained close to Antarctica, but climatic changes after the departure of Australia, particularly the steady development of the Antarctic ice cap and falling Southern Ocean temperatures (Kemp 1984), changed distributions and abundances. The bioclimatic upheavals that took place as Australia drifted northwards are well documented for the flora and marsupials (Archer 1984; Kemp 1984; Martin 1984), but scant attention has been given to the likely effects this must have had on bat zoogeography. The only notable exception is Hand (1984b);

The tectonics of the collision zone between the Indo-Australian Plate and the Asian Plate and/or platelets are very complex (Cracraft 1980; Audley-Charles 1981; Lee & McCabe 1986). Probably, a range of islands and the northern edge of New Guinea (part of the Australia Plate) began emerging soon after Australia left Antarctica. Dispersal to or from Australia via the north was probably open from about the Late Oligocene or Early Miocene onwards. Vespertilionid bats, therefore, could have arrived or left Australia early in the evolution of the modern genera. Changes in climate accompanying Australia’s northwards drift have complicated the story.

The classical arguments suggest most, if not all, of Australia’s vespertilionid genera are derived by invasion from the north. Some inferences have been made regarding southern origins for some genera, but there are always counter-hypotheses suggesting northern affinities. The resolution of these often conflicting views is hampered by the lack of thorough phylogenetic studies for the majority of the vespertilionid genera in Australia. The complex and as yet incompletely understood tectonic history of the Australian continent sets the chronological and geographical constraints on the evolution of Australia’s vespertilionid bat fauna.

### Affinities within the Vespertilionidae

The species-level taxonomy of Australia’s vespertilionids remains unsettled, as does the study of the affinities of the unique and Australian-centred genera *Chalinolobus*, *Nyctophilus*, *Scotorepens* and *Scoteanax*. With the notable exception of reviews by Kitchener & Caputi (1985) and Kitchener, Caputi &



Jones (1986), no significant progress has been made in determining the phylogenetic relationships of these Australo-centric genera since the work of Tate (1941d, 1941e, 1942).

### Fossil Record

The oldest known bat fossils have been found in the Early to Middle Eocene deposits of North America, Europe and the Middle East. Among these is the 50 million year-old *Icaronycteris index*, the oldest and best preserved of all bat fossils (Jepsen 1966). It exhibits a complete and typical complement of adaptations for flight, indicating that the origin of bats predates the Eocene and since that time most osteological characters of bats have undergone only minor changes (Walton & Walton 1970).

As Hand (1984b) suggested in her phylogenetic interpretation of bats, the oldest fossil to be properly assigned to the Superfamily Vespertilionoidea is *Stehlinia*, found in the Middle Eocene of Europe. Despite these relatively early origins, the Vespertilionidae, along with the Mystacinidae and Molossidae, are the most advanced bat families (Miller 1907). While the Vespertilionidae has the broadest distribution of any modern family of bats and is found on all continents except Antarctica, it probably had its origins in the Old World tropics of either Asia or Africa. This is substantiated by the greater number and diversity of vespertilionids in the Old World and by a generally earlier fossil occurrence there (for summary see Hall 1984; Hand 1984b).

Like most microchiropteran bats, vespertilionids are a morphologically conservative group of mammals (Adams *et al.* 1982; Hand 1984b); many species found in the early Tertiary can be readily assigned to modern genera. Butler (1978) pointed out that by the Late Pliocene, the Vespertilionidae already had reached its present dominance in Africa and that among the six forms recovered from deposits of eastern and southern Africa were representatives of the modern vespertilionid genera *Miniopterus*, *Pipistrellus* and *Nycticeius*.

The morphological conservatism of the Vespertilionidae has meant that very few clues to the recent evolutionary past of the group can be found. In Australia, fossils demonstrate how vespertilionids have not only have been conservative in their morphology, but also in their distributions. Subfossil and Pleistocene cave deposits examined by Wakefield (1963a, 1963b, 1964b, 1967a), Tidemann (1967) and Maddock (1971) revealed several vespertilionid species, all within their present range. Only one species, *Nyctophilus howensis* (McKean 1975), is known to have become extinct in Australia and only two genera, *Chalinolobus* and *Nyctophilus*, underwent notable radiation. Morphological and distributional patterns are thus difficult to interpret in terms of species history.

The best known bat fossils in Australia come from Miocene deposits in South Australia and north-western Queensland (Archer 1978; Hand 1984b). Discoveries from the Riversleigh deposit in Queensland have been useful in revealing a line between the Australian hipposiderid fossils and the fossil subgenus *Brachipposideros* from France (Hand 1984b), but the deposit contains no vespertilionid fossils. The eleven vespertilionid genera present within Australia are likely to have arrived along several different routes and on several occasions before achieving their current distributions. These dispersal events, at least for *Chalinolobus*, *Eptesicus*, *Miniopterus*, *Nyctophilus* and *Falsistrellus*, probably occurred before the Pleistocene. This can be inferred from the fact that fossils found in numerous and widely distributed Pleistocene cave deposits are referable to modern species of these genera (Archer, Clayton & Hand 1984).

## COLLECTION AND PRESERVATION

### Collection

An excellent review of bat-capturing techniques can be found in Helman & Churchill (1986). The cave and mine-dwelling species of the Vespertilionidae are easiest to catch during the winter months when they frequently enter periods of torpor. Torpor is more pronounced in higher latitudes and altitudes. In summer, when bats are active and alert at their roost they can be captured by mist-netting narrow passageways or the entrance to a cave or mine.

Forest bats are collected by mist-netting, bat-trapping, trip wires and spotlight shooting (Helman & Churchill 1986). The diversity of vespertilionids requires a correspondingly diverse set of catching techniques. Slow-flying species can easily detect mist-nets and are usually caught in bat traps (Tidemann & Woodside 1978). Collecting is most successful in summer months when all bats are active. As most bats require an evening drink, the best catching sites are near or over water. Whereas spotlight shooting of small bats is an effective way of acquiring specimens, specimen damage is often severe.

### Preservation

Since the vespertilionids are small mammals, they can be preserved by placing wholly in 70% ethyl alcohol containing 2% glycerine. The body cavity should be cut open to allow penetration of alcohol. Preparation of skins is best done from freshly collected material although study skins can be prepared from frozen specimens. The large ears of the nyctophylids require special attention in the preparation of study skins.

### Maintenance in captivity

Rasweiler (1977) gives an extensive review of the literature relating to Chiroptera in captivity. Several reports of Australian vespertilionids in captivity (Ryan 1963a; Hall 1982a; Humphrey-Smith 1982) show that on a short-term basis, vespertilionids are easy to maintain in captivity. The most common food used is mealworms (*Tenebrio molitor*), but long-term dietary deficiencies can develop when cultured insects are used (Rasweiler 1977).

Because of their small size, vespertilionids can be housed in rooms or 'bird-cage' type structures. The bats need a confined dark area such as a hollow log, a sheet of hessian or a small box to roost in during the day. Different species have quite separate microclimatic requirement for their roosts (Rasweiler 1977), but all seem to need high humidities and the roost to be draught-free.

## CLASSIFICATION

### Subfamily Vespertilioninae

*Chalinolobus*: This genus has a Australian-centred distribution, but also has suggested affinities to geographically distant taxa. Since its description by Peters (1866a), based on records of *Vespertilio tuberculatus* Forster from New Zealand, Dobson (1875) established the name *Glauconycteris* as a subgenus of *Chalinolobus* to include African forms he believed were allied closely. Ryan (1966) considered subgeneric rank unwarranted and argued for its replacement by *Chalinolobus*. Van Deusen & Koopman (1971) concluded, however, that at least subgeneric status for *Glauconycteris* is justified. Neither Ryan nor Van Deusen & Koopman questioned the supposed affinity between the two groups.

Hill (1983) mentioned the striking similarities in both skull morphology and external features of the Malaysian *Pipistrellus societatus* to those of *Chalinolobus* of the Australian region and less distinctly, to similar features of the African subgenus *Glauconycteris*. This included the presence of the lobe at the angle of the mouth that was a diagnostic feature of the genus and from which its name is derived. This feature has also been noted in a newly described sister species to *P. societatus*, *P. coprosus* (Hill & Francis 1984). Hill in Hamilton-Smith (1975) is reported as suggesting a link between *Chalinolobus* and *Glauconycteris* and *Hesperopterus* of Asia, but he did not pursue this view in a subsequent work (Hill 1983). The observations of Hill (1983) thus set up two contrapuntal views for the affinities of this group. That is, northern pipistrelloid origins, at least for *Chalinolobus*, or a southern, perhaps Gondwanan link between *Glauconycteris* and *Chalinolobus*. This latter seems unlikely given that Africa separated from other Gondwanan elements about 90 mybp (Audley-Charles, Hurley & Smith 1981).

*Eptesicus*: The Australian representatives of this genus are separated from their nearest congeners in Malaysia by about 3000 km (Tate 1942; Campbell & Kitchener 1980). Despite this extreme degree of isolation, Miller (1907) had no hesitation in stating that, apart from the smaller size of the Australian *Eptesicus*, they were the same in essential details to larger members of the genus in the Americas and Europe. Miller (1907), Tate (1942) and Koopman (1984a) argued that *Eptesicus* as a whole is a pipistrelloid offshoot. Hill & Francis (1984) cited karyological evidence from Heller & Volleth (1984) that seems to closely align Australian *Eptesicus* with *E. capensis* of southern Africa, a view held by Koopman (1975) on morphological grounds, and *Pipistrellus* from south-eastern Asia. In fact, Heller & Volleth argued for synonymy between *Eptesicus* from Australia and *Pipistrellus*. Conversely, in a study of the karyotypic patterns of North American examples of *Pipistrellus* and *Eptesicus*, Bickam (1979) concluded that these genera exhibit divergent karyotypes and, therefore, are quite distinct. These divergent conclusions suggest a number of possibilities that must be investigated. They are:

North American and, by implication, Eurasian *Eptesicus* are not related closely to Australian congeners and the morphological similarities between them are due to convergence;

the South African *Eptesicus capensis* may be either an independent offshoot of *Pipistrellus* with convergent karyotype and phenotype;

Australian and South African species are sister taxa, vicariously separated on fragments of Gondwana. This seems unlikely, however, owing to the early separation of Africa and the inferred sister species relationship.

Recent taxonomic reviews of the Australian forms (Campbell & Kitchener 1980; Carpenter, McKean & Richards 1978; Kitchener 1976a; McKean, Richards & Price 1978; Tidemann *et al.* 1981) have increased the number of Australian species, but the problem of the true affinities of *Eptesicus* in Australia has not been resolved.

*Myotis*: Only *Myotis adversus* is currently recognised from Australia. It is divided into subspecies: *M. a. moluccarum* from northern Australia and *M. a. macropus* from eastern Australia. The species is distributed in a narrow band around the coast from near Port Hedland, Western Australia to near the South Australia-Victoria border (McKean & Hall 1965; Hall & Richards 1979). This bat never penetrates far inland and always roosts near bodies of fresh water (McKean & Hall 1965; Richards 1983c).

As a member of the subgenus *Leuconoe* (see Findley 1972 for defining characters), *Myotis adversus* must be seen as a southerly extension of a group whose distribution and diversity centre on Sumatra and Borneo in the

Indonesian Archipelago. Various subspecies of *M. adversus* are found from Java to Vanuatu and south to Australia (Tate 1941d; Koopman 1982; Hill 1983). Hill (1983) gave a most useful account of the current taxonomy of this group.

The affinities of *Myotis* in Australia are undoubtedly with those of south-eastern Asia and the Indonesian Archipelago. All current taxonomic evidence suggests overwater dispersal into Australia from the north, with only limited radiation of endemic forms.

*Scotorepens* and *Scoteanax*: These two Australian genera have been the subject of some debate. Following Miller (1907), Tate (1942) provisionally grouped all Australian forms under the genus *Scoteinus*. Tate commented that this grouping was probably polyphyletic. He also noted that the largest Australian species in the group, *S. rueppellii*, was unlike any other Australian nycticeine. Troughton (1941) erected the genus *Scoteanax* to accept *rueppellii* and the genus *Scotorepens* to accommodate the remaining Australian species. Most authors followed Tate (1942) until Koopman (1978) recognised *Scoteanax* and *Scotorepens* as subgenera of the predominantly New World *Nycticeius*.

A recent major review of the genus *Nycticeius* (as it was then named) in Australia by Kitchener & Caputi (1985) resurrected the subgenera of Troughton (1941) and presented the only published objective phylogeny for an Australian genus. Their analysis indicated that *Scoteanax* has strong affinities with *Scotomanes* and lesser ones to *Scotophilus*. Both these genera are African and south-east Asian in distribution. On the other hand, *Scotorepens* linked most strongly with *Nycticeius* (here restricted to the Americas) and then to *Scotoecus* of south-eastern Asia and *Rhogeessa* of the Americas. Of note is the fact that Kitchener & Caputi's (1985) analysis shows the closest relatives of each Australian genus lie outside Australia and that *Scoteanax* and *Scotorepens* are not sister groups, but related only distantly. The strong divergence between the two groups in Australia is noted by Tate (1942). He drew no conclusions, however, regarding the affinities of the Australian forms.

*Pipistrellus* and *Falsistrellus*. That there are two distinct groupings of Australian pipistrelles has long been recognised, the smaller forms, clearly related to species in south-eastern Asia, the Indonesian Archipelago and New Guinea and a larger, less clearly related form restricted to southern Australia (Tate 1942). Troughton (1941) erected the genus *Falsistrellus* to contain the larger, southern species. Kitchener *et al.* (1986) have supported Troughton's view.

The phenetic and phylogenetic analyses in the latter work closely link the Australian and Papuan small species as a monophyletic group. The smaller Australian forms, retained in the genus *Pipistrellus* by Kitchener *et al.* (1986), are clearly part of the web of species extending throughout the Indo-Australian region (see earlier taxonomic reviews of Tate 1942; Koopman 1973) as demonstrated by the inclusion of *P. imbricatus* and *P. javanicus* in the Wagner tree analysis. The affinities of *Falsistrellus*, however, are not fully resolved. Although Kitchener *et al.* (1986) suggested common ancestry between *Falsistrellus* and *Pipistrellus*, they did not include any of the other possibly closely related genera in the phylogenetic analysis, and thus failed to show conclusively that the Australian *Pipistrellus* and *Falsistrellus* form a monophyletic group. This must await an analysis of much wider scope, in particular, one designed to resolve the uncertain affinities and status of such genera as *Eptesicus*, *Pipistrellus*, *Vespertilio*, *Ia* and *Glischropus* (Tate 1942; Corbet 1978). Koopman (1984a) stated that he was unable to identify the affinities of *Falsistrellus*, but notes that it is not related closely to *Pipistrellus tenuis*.

A further interesting implication of the Wagner tree of Kitchener *et al.* (1986) is that the two Australian pipistrelles included are not sister species, but have separate sister species in New Guinea.



### Subfamily Murinae

*Murina*: The genus *Murina* has only recently been recorded from Australia (Richards *et al.* 1982). They assigned the sole Australian specimen to the species *Murina florum* which is found in New Guinea and adjacent islands to the west of New Guinea (Tate 1941e; Hill 1983). The species-level taxonomy of this genus, however, is unsettled and the species name of the Australian form may change. Corbet & Hill (1980) listed eleven species, but Honacki, Kinman & Koepl (1982) recognised fifteen.

Whatever the species name assigned to the Australian representatives of this genus may be, there is no doubt that, on the present evidence, it represents an outlier to the central region of diversity for the genus, south-eastern Asia (including Japan) and the Indonesian Archipelago. Useful reviews of the taxonomy and distribution of the genus are found in Tate (1941e), Hill (1983), and Hill & Francis (1984). The affinities of the Australian *Murina* species lie with New Guinea and beyond.

### Subfamily Kerivoulinae

*Phoniscus*. Golden-tipped Bats are relatively rare in Australia, despite a number of recent records and a substantial range extension (Lunney & Barker 1986). The affinities are again towards the north, since the Australian population must be seen as an outlier of a group dispersed widely in south-eastern Asia, the Indonesian Archipelago and New Guinea.

The subfamily seems to be a sister-group of the genus *Myotis*. Tate (1941d) suggested common ancestry between the *Myotis* line and the kerivoulinae line. Van Valen (1979) is less specific, having suggested only that the kerivoulinae represent an offshoot of a *Myotis*-like vespertilionine form, but placed the Kerivoulinae in the Natalidae. This is still within the superfamily Vespertilionoidea, but rather remote from the Vespertilionidae where they are placed traditionally. Sigé (1974) elevated the Kerivoulinae to family status and included in it the European Middle Eocene to Early Oligocene *Stehlinia*. The views of Van Valen & Sigé have not been widely adopted.

### Subfamily Nyctophilinae

*Nyctophilus*. This diverse and widespread Australia-centred genus has long been recognised as deserving of at least subfamilial rank (Miller 1907; Tate 1941e). The North and Central American genera *Antrozous* and *Bauerus*, together with the New Guinea genus *Pharotis*, are usually placed in the same subfamily. Koopman (1970) commented that the American genera were probably not 'specially related' to the Australian and New Guinea genera, but failed to give supporting evidence or arguments.

Pine *et al.* (1971) presented evidence to suggest that *Nyctophilus* has no special relationship to North American genera, such as *Antrozous* and *Bauerus*. This opinion is based on dissimilarities of external penial morphology. In fact, Koopman (*in* Pine, Carter & La Val 1971) pointed out the closeness of penial morphology between *Otonycteris* of the Old World and *Antrozous*. Koopman is cited as suggesting that for this and other unspecified reasons, *Otonycteris* and *Antrozous* are closely related. After showing that the penial morphology of *Nyctophilus* and *Pharotis* from the Australian region is different to the form found in *Otonycteris* and *Antrozous*, Pine *et al.* (1971) concluded that there is indeed no special relationship between the two groups. For unspecified reasons, Hill & Smith (1984) have not followed this interpretation and continue to show *Antrozous* and allies as members of the subfamily Nyctophylinae.

There is neither thorough phylogenetic nor fossil evidence in favour of either hypothesis, although it should be noted that no-one has suggested a northern origin for the genus in Australia. A sister-group or potential ancestor for *Nyctophilus* has not been identified in the south-east Asian region.

### Subfamily **Miniopterinae**

*Miniopterus*. This genus has an Old World distribution with greatest diversity in the Asian and Indonesian regions. The taxonomy of the genus is unsettled, with at least four partly inconsistent views expressed in the literature. In the Australian context, there are four arrangements:

Tate (1941e) : *Miniopterus schreibersii blepotis* – eastern coast of Australia and extending into New Guinea and beyond; *M. s. orianae* for the indisputably different Northern Territory form; and *M. australis* – eastern coast of Australia, New Guinea and islands to the east of New Guinea.

Maeda (1982) : *M. oceanensis* Maeda 1982 – eastern coast of Australia, the Moluccas, New Guinea and Solomon Islands; *M. schreibersii* – Northern Territory form; *M. australis* - eastern coast and beyond.

Koopman (1982) : *M. schreibersii* – Australia, no mention being made of the status of subspecies; *M. australis*.

Hill (1983) : *M. schreibersii oceanensis* – distribution following Maeda (1982); *M. s. orianae* – Northern Territory; *M. australis* – as above. This arrangement is adopted by Koopman (1984a).

The classification of Maeda (1982) received trenchant criticism from Hill (1983) and Koopman (1984a) and has not been widely adopted (see for example, Strahan 1983).

The general consensus regarding the origins and affinities of *Miniopterus* in Australia seems to implicate invasion from the north during the late Tertiary. Hall (1981) postulated two invasion pathways into Australia to account for the current distribution of subspecies or populations, such as that at Naracoorte, South Australia, which shows aberrant reproductive behaviour.

## LITERATURE CITED

- Adams, M., Baverstock, P.R., Tidemann, C.R. & Woodside, D.P. (1982). Large genetic differences between sibling species of bats *Eptesicus* from Australia. *Heredity* 48: 435-438
- Anthony, E.L.P. & Kunz, T.H. (1977). Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* 58: 775-786
- Archer, M. (1978d). Australia's oldest bat, a possible rhinolophid. *Proceedings of the Royal Society of Queensland* 89: 23
- Archer, M. (1984e). Earth-shattering concepts for historical zoogeography. Pp. 45-67 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Archer, M., Clayton, G. & Hand, S. (1984). A checklist of Australasian fossil mammals. Pp. 1027-1082 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Audley-Charles, M.G. (1981). Geological history of the region of Wallace's line. Pp. 24-35 in Whitmore, T.C. (ed.) *Wallace's Line and Plate Tectonics*. Oxford: Clarendon Press

- Audley-Charles, M.G., Hurley, A.M. & Smith, A.G. (1981). Continental movements in the Mesozoic and Cenozoic. Pp. 9-23 in Whitmore, T.C. (ed.) *Wallace's Line and Plate Tectonics*. Oxford: Clarendon Press
- Barbour, R.W. & Davis, W.H. (1969). *Bats of America*. Lexington: University Press of Kentucky : Lexington 286 pp.
- Barbu, P. (1960). *Contributii la studiulmonografic al lui Miniopterus schreibersii Kuhl. Bucharesti Universitates "C.I. Parlov", Analele (Seria Stiintele Naturii)* 24: 83-107
- Barclay, R.M.R. (1985a). Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. *Canadian Journal of Zoology* 63: 2507-2515
- Barclay, R.M.R. (1985b). Marking and observational techniques. In Kunz, T.H. (ed.) *Behavioral and Ecological Methods for the Study of Bats*. Smithsonian Institution Press : Washington, D.C.
- Bell, G.P. (1980b). Habitat use and responses to patches of prey by desert insectivorous bats. *Canadian Journal of Zoology* 58: 1876-1883
- Bell, G.P. (1982). Behavioural and ecological aspects of gleaning by a desert insectivorous bat, *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behavioural Ecology and Sociobiology* 10: 217-223
- Belwood, J.J. & Fenton, M.B. (1976). Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 54: 1674-1678
- Belwood, J.J. & Fullard, J.H. (1984). Echolocation and foraging behaviour in the Hawaiian Hoary Bat, *Lasiurus cinereus semotis*. *Canadian Journal of Zoology* 62: 2113-2130
- Bickham, J.W. (1979). Chromosomal variation and the evolutionary relationships of vespertilionid bats. *Journal of Mammalogy* 60: 350-363
- Black, H.L. (1974). A north temperate bat community: structure and prey populations. *Journal of Mammalogy* 55: 138-157
- Bradbury, J.W. (1977a). Lek mating behaviour in the Hammer-headed Bat. *Zeitschrift für Tierpsychologie* 45: 225-255
- Bradbury, J.W. (1977b). Social organisation and communication. Pp. 1-72 in Wimsatt, W.A. (ed.) *Biology of Bats*. Vol. 2. New York: Academic Press
- Braithwaite, R.W., Winter, J.W., Taylor, J.A. & Parker, B.S. (1985). Patterns of diversity and structure of mammalian assemblages in the Australian tropics. *Australian Mammalogy* 8: 170-186 [47]
- Breed, W.G. & Inns, R.W. (1985). Variation in sperm morphology of Australian Vespertilionidae and its possible phylogenetic significance. *Mammalia* 49: 105-18
- Butler, P.M. (1978). Insectivora and Chiroptera. Pp. 56-68 in Maglio, V.J. & Cooke, H.B.S. (eds) *Evolution of African Mammals*. Harvard University Press : Cambridge
- Campbell, N.A. & Kitchener, D.J. (1980). Morphological divergence in the genus *Eptesicus* (Microchiroptera: Vespertilionidae) in Western Australia: a multivariate approach. *Australian Journal of Zoology* 28: 457-474
- Carpenter, S.M., McKean, J.L. & Richards, G.C. (1978). Multivariate morphometric analysis of *Eptesicus* (Mammalia: Chiroptera) in Australia. *Australian Journal of Zoology* 26: 629-638
- Carter, D.C. (1970). Chiropteran reproduction. Pp. 233-246 in Slaughter, B.H. & Walton, D.W. (eds) *About Bats. A Chiropteran Symposium*. Southern Methodist University Press : Dallas

- Churchill, S.K., Hall, L.S. & Helman, P.M. (1984). Observations on Longeared Bats (Vespertilionidae: *Nyctophilus*) from northern Australia. *Australian Mammalogy* 7: 17-28
- Clark, A.J. (1927). *Comparative Physiology of the Heart*. MacMillan : London 242 pp.
- Clark, D.R. Jr., Kunz, T.H. & Kaiser, T.E. (1978). Insecticides applied to a nursery colony of Little Brown Bats (*Myotis lucifugus*): lethal concentrations in brain tissues. *Journal of Mammalogy* 59: 84-91
- Cogger, H. & Heatwole, H. (1984). The Australian reptiles: origins, biogeography, distribution patterns and island evolution. Pp. 343-370 in Archer, M. & Clayton, A. (eds) *Vertebrate Zoogeography and Evolution in Australia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Constantine, D.G. (1970). Bats in relation to the health, welfare and economy of man. Pp. 319-449 in Wimsatt W.A. (ed.) *Biology of Bats*. Vol. 2. New York: Academic Press
- Corbet, G.B. (1978). *The Mammals of the Palaearctic Region. A taxonomic review*. London: British Museum 314 pp.
- Corbet, G.B. & Hill, J.E. (1980). *A World List of Mammalian Species*. London: British Museum xiii 226 pp.
- Cracraft, J. (1980). Biostratigraphic patterns of terrestrial vertebrates in the south western Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* 32: 353-369
- CSIRO (1983). Division of Applied Physics Biennial Report 1981-1983. 129 pp.
- Daniel, M.J. & Williams, G.R. (1981). Long-tailed Bats (*Chalinolobus tuberculatus*) hibernating in farm buildings near Geraldine, South Canterbury. *New Zealand Journal of Zoology* 8: 425-430
- Davis, W.H., Barbour, R.W. & Hassell, M.D. (1968). Colonial behaviour of *Eptesicus fuscus*. *Journal of Mammalogy* 49: 44-50
- Dobson, G.E. (1875). On the genus *Chalinolobus*, with descriptions of new or little-known species. *Proceedings of the Zoological Society of London* 1875: 381-388
- Dobson, G.E. (1878). *Catalogue of the Chiroptera in the Collection of the British Museum*. British Museum : London xlii 567 pp. 30 pls
- Dwyer, P.D. (1963a). The breeding biology of *Miniopterus schreibersii blepotis* (Temminck) (Chiroptera) in north-eastern New South Wales. *Australian Journal of Zoology* 11: 219-40
- Dwyer, P.D. (1963b). Seasonal changes in pelage of *Miniopterus schreibersii blepotis* (Chiroptera) in north-eastern New South Wales. *Australian Journal of Zoology* 11: 290-300
- Dwyer, P.D. (1964a). Seasonal changes in activity and weight of *Miniopterus schreibersii blepotis* (Chiroptera) in north-eastern New South Wales. *Australian Journal of Zoology* 12: 52-69
- Dwyer, P.D. (1964b). Fox predation on cave bats. *Australian Journal of Science* 26: 397-398
- Dwyer, P.D. (1965a). Flight patterns of some eastern Australian bats. *Victorian Naturalist* 82: 37-41 [40]
- Dwyer, P.D. (1965b). Bat erosion in Australian limestone caves. *Helictite* 3: 85-90
- Dwyer, P.D. (1966a). Mortality factors of the Bent-winged Bat. *Victorian Naturalist* 83: 31-36

- Dwyer, P.D. (1966b). The population pattern in *Miniopterus schreibersii* (Chiroptera) in south-eastern New South Wales. *Australian Journal of Zoology* 14: 1073-1137
- Dwyer, P.D. (1966c). Observations on *Chalinolobus dwyeri* (Chiroptera: Vespertilionidae) in Australia. *Journal of Mammalogy* 47: 716-718
- Dwyer, P.D. (1968). The biology, origin, and adaptation of *Miniopterus australis* (Chiroptera) in New South Wales. *Australian Journal of Zoology* 16: 49-68
- Dwyer, P.D. (1969). Population ranges of *Miniopterus schreibersii* (Chiroptera) in south-eastern Australia. *Australian Journal of Zoology* 17: 665-86
- Dwyer, P.D. (1970a). Foraging behaviour of the Australian large-footed *Myotis* (Chiroptera). *Mammalia* 34: 76-80
- Dwyer, P.D. (1970b). Latitude and breeding season in a polyoestrus species in *Myotis*. *Journal of Mammalogy* 51: 405-410
- Dwyer, P.D. (1971). Temperature regulation and cave dwelling in bats: an evolutionary perspective. *Mammalia* 35: 424-453
- Dwyer, P.D. & Hamilton-Smith, E. (1965). Breeding caves in maternity colonies of Bent-winged Bat in south-eastern Australia. *Helictite* 4: 3-21
- Dwyer, P.D. & Harris, J.A. (1972). Behavioural acclimatization to temperature by pregnant *Miniopterus* (Chiroptera). *Physiological Zoology* 45: 14-21
- Fenton, M.B. (1974). Role of echolocation in the evolution of bats. *American Naturalist* 108: 386-388
- Fenton, M.B. (1977). Variation in the social calls of Little Brown Bats (*Myotis lucifugus*). *Canadian Journal of Zoology* 55: 1151-1157
- Fenton, M.B. (1980). Adaptiveness and ecology of echolocation in terrestrial (aerial) systems. Pp. 427-448 in Busnel, R.G. & Fish, J.F. (eds) *Animal Sonar Systems NATO Advanced Study Institute Series A. Vol. 2*. New York: Plenum Press
- Fenton, M.B. (1982a). Echolocation, insect hearing and feeding ecology of insectivorous bats. Pp. 261-285 in Kunz, T.H. (ed.) *Ecology of Bats*. New York: Plenum Press [43]
- Fenton, M.B. (1982b). Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, north Queensland. *Australian Journal of Zoology* 30: 417-425
- Fenton, M.B. (1984). Echolocation: implications for ecology and evolution of bats. *Quarterly Review of Biology* 58: 33-53
- Fenton, M.B. & Bell, G.P. (1979). Echolocation and feeding in four species of *Myotis* (Chiroptera). *Canadian Journal of Zoology* 57: 1271-1277
- Fenton, M.B. & Bell, G.P. (1981). Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy* 62: 233-243
- Fenton, M.B. & Morris G.K. (1976). Opportunistic feeding by desert bats (*Myotis* spp.). *Canadian Journal of Zoology* 54: 526-530
- Fenton, M.B., Belwood, J.J., Fullard, J.H. & Kunz, T.H. (1976). Responses of *Myotis lucifugus* (Chiroptera: Vespertilionidae) to calls of conspecifics and to other sounds. *Canadian Journal of Zoology* 54: 1443-1448
- Findley, J.S. (1972). Phenetic relationships among bats of the genus *Myotis*. *Systematic Zoology* 21: 31-52
- Forman, G.L. (1972). Comparative morphological and histochemical studies of stomachs of selected American bats. *University of Kansas Scientific Bulletin* 49: 591-729



- Foster, G.W., Humphrey, S.R. & Humphrey, P.P. (1978). Survival rates of young Southeastern Brown Bats, *Myotis austroriparius* in Florida. *Journal of Mammalogy* 59: 299-304
- Funakoski, K. & Uchida, T.A. (1978). Studies on the physiological and ecological adaptations of temperate insectivorous bats. II Hibernation and winter activity in some cave-dwelling bats. *Japanese Journal of Ecology* 28: 237-261
- Gates, J.E., Feldhamer, G.A., Griffith, L.A. & Raesly, R.L. (1984). Status of cave-dwelling bats in Maryland: importance of marginal habitats. *Wildlife Society Bulletin* 12: 162-169
- Gill, T. (1872). On the characteristics of the primary groups of the class of mammals. *Proceedings of the American Association for the Advancement of Science* 20: 284-306
- Goodwin, G.C. & Greenhall, A.M. (1961). A review of the bats of Trinidad and Tobago - Description, rabies infection and ecology. *Bulletin of the American Museum of Natural History* 122: 137-302
- Gould, E. (1971). Studies of maternal-infant communication and development of vocalizations in the bats *Myotis* and *Eptesicus*. *Communication of Behavioural Biology Part A* 5(5): 263-313
- Gray, J.E (1821). On the natural arrangement of vertebrate animals. *London Medical Repository* 15: 296-310
- Green, R.H. (1965). Observations on the Little Brown Bat, *Eptesicus pumilus* Gray, in Tasmania. *Records of the Queen Victoria Museum* 20: 1-16 3 figs 2 pls
- Green, R.H. (1966). Notes on the Lesser Long-eared Bat, *Nyctophilus geoffroyi*, in northern Tasmania. *Records of the Queen Victoria Museum* 22: 1-4
- Griffin, D.R. (1958). *Listening in the Dark*. New Haven: Yale University Press xviii 413 pp.
- Griffin, D.R. & Galambos, R. (1940). Obstacle avoidance by flying bats. *Anatomical Record* 78: 95
- Griffin, D.R. & Galambos, R. (1941). The sensory basis of obstacle avoidance by flying bats. *Journal of Experimental Zoology* 86: 481-506
- Gustin, M.K. & McCracken, G.F. (1986). Scent recognition between females and pups in the bat *Tadarida brasiliensis mexicana*. *Animal Behaviour* 35: 13-19
- Hall, L.S. (1981). The biogeography of Australian bats. Pp. 1557-1583 in Keast, A. (ed.) *Ecological Biogeography of Australia*. Vol. 2. The Hague: Junk
- Hall, L.S. (1982a). Management of Microchiroptera in captivity. Pp. 157-160 in Evans, D.D. (ed.) *The Management of Australian Mammals in Captivity*. Zoological Parks Board of Victoria : Melbourne
- Hall, L.S. (1982b). Common Bent-winged Bat *Miniopterus schreibersii*: maintenance of a large colony. Pp. 172-174 in Evans, D.D. (ed.) *The Management of Australian Mammals in Captivity*. Melbourne: Zoological Parks Board of Victoria
- Hall, L.S. (1982c). The effect of cave microclimate on winter roosting behaviour in the bat *Miniopterus schreibersii blepotis*. *Australian Journal of Ecology* 7: 129-136
- Hall, L.S. (1984). And then there were bats. Pp. 837-852 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia*. (Animals in Space & Time). Hesperian Press : Carlisle
- Hall, L.S. & Richards, G.C. (1979). *Bats of Eastern Australia*. Queensland Museum Booklet No. 12 vi 66 pp.

- Hamilton-Smith, E. (1975). Gondwanaland and the Chiroptera. *Australian Mammalogy* 1: 382-383
- Hamilton-Smith, E. (1978). Endangered and threatened Chiroptera of Australia and the Pacific Region. Pp. 86-100 in Tyler, M.J. (ed.) *The Status of Endangered Australian Wildlife*. Adelaide: Royal Zoological Society of South Australia
- Hand, S.J. (1984b). Bat beginnings and biogeography: a southern perspective. Pp. 853-903 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Heller, K.-G. & Volleth, M. (1984). Taxonomic position of “*Pipistrellus societatus*” Hill (1972) and the karyological characters of the genus *Eptesicus* (Chiroptera: Vespertilionidae). *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 22: 65-77
- Helman, P. & Churchill, S. (1986). Bat capture techniques and their use in surveys. *Macroderma* 2(2): 32-53
- Herd, R.M. & Fenton M.B. (1983). An electrophoretic, morphological and ecological investigation of a putative hybrid zone between *Myotis lucifugus* and *Myotis yumanensis* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 61: 2029-2050
- Herskovitz, P. (1972). The recent mammals of the Neotropical region: a zoogeographic and ecological review. Pp. 311-431 in Keast, A., Erk, C. & Glass, B. (eds) *Evolution, Mammals and Southern Continents*. New York: State University of New York Press
- Hill, J.E. (1983). Bats (Mammalia : Chiroptera) from Indo-Australia. *Bulletin of the British Museum Natural History (Zoology)* 45: 103-208
- Hill, J.E. & Francis, C. (1984). New bats (Mammalia: Chiroptera) and new records of bats from Borneo and Malaya. *Bulletin of the British Museum of Natural History (Zoology)* 47: 305-379
- Hill, J.E. & Pratt, T.K. (1981). A record of *Nyctophilus timoriensis* from New Guinea. *Mammalia* 45: 264-266
- Hill, J.E. & Smith, J.D. (1984). *Bats a Natural History*. British Museum : London 243 Pp.
- Holloway, J.D. & Jardine, N. (1968). Two approaches to zoogeography: a study based upon the distribution of butterflies, birds and bats in the Indo-Australian area. *Proceedings of the Linnean Society of London* 179: 153-158
- Honachki, J.H., Kinman, K.E. & Koeppl, J.W. (1982). *Mammal Species of the World. A taxonomic and geographic reference*. Allen Press : Lawrence and Association of Systematic Collections ix 694 pp.
- Humphrey-Smith, I. (1982). Survival of captive Microchiroptera feeding on prey attracted to artificial lights. Pp. 164-171 in Evans, D.D. (ed.) *The Management of Australian Mammals in Captivity*. Melbourne: Zoological Parks Board of Victoria
- Jespen, G.L. (1966). Early Eocene bat from Wyoming. *Science* 154: 1333-1339
- Johnson, D.H. (1964) Mammals of the Arnhem Land Expedition. Pp. 427-515 in Spect, R.L. (ed.) *Records of the American-Australian Scientific Expeditions to Arnhem Land*. Zoology. Melbourne Vol. 4
- Jones, C. (1967). Growth, development, and wing loading in the Evening Bat, *Nycticeius humeralis* (Rafinesque). *Journal of Mammalogy* 48: 1-19
- Kallen, F.C. (1977). The cardiovascular systems of bats: structure and function. Pp. 289-483 in Winsatt, W.A. (ed.) *Biology of Bats. Vol. 3*. New York : Academic Press

- Kay, L. (1980). Air sonars with acoustical display of spatial information. Pp. 769-816 in Busnel, R.G. & Fish, J.F. (eds) *Animal Sonar Systems*. NATO Advanced Study Institute Series A, Vol. 28. New York: Plenum Press
- Keast, A. (1972a). Australian mammals: zoogeography and evolution. Pp. 195-246 in Keast, A., Erk, C. & Glass, B. (eds) *Evolution, Mammals and Southern Continents*. New York: State University of New York Press
- Keast, A. (1972b). Comparisons of contemporary mammal faunas of southern continents. Pp. 433-501 in Keast, A., Erk, C. & Glass, B. (eds) *Evolution, Mammals and Southern Continents*. New York: State University of New York Press
- Kemp, E. (1984). Tertiary palaeogeography and the evolution of Australian climate. Pp. 61-68 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Carlisle: Hesperian Press
- Kitchener, D.J. (1975). Reproduction of Gould's Wattled Bat *Chalinolobus gouldii* (Gray) (Vespertilionidae) in Western Australia. *Australian Journal of Zoology* 23: 29-42
- Kitchener, D.J. (1976a). *Eptesicus douglasi*, a new vespertilionid bat from Kimberley, Western Australia. *Records of the Western Australian Museum* 4: 295-301
- Kitchener, D.J. & Caputi, N. (1985). Systematic revision of Australian *Scoteanax* and *Scotorepens* (Chiroptera: Vespertilionidae) with remarks on relationships to other Nycticeini. *Records of the Western Australian Museum* 12: 85-146
- Kitchener, D.J. & Coster, P. (1981). Reproduction in female *Chalinolobus morio* (Gray) (Vespertilionidae) in south-western Australia. *Australian Journal of Zoology* 29: 305-320
- Kitchener, D.J. & Halse, S.A. (1978). Reproduction in female *Eptesicus regulus* (Thomas) (Vespertilionidae) in south-western Australia. *Australian Journal of Zoology* 26: 257-267
- Kitchener, D.J., Caputi, N. & Jones, B. (1986). Revision of Australo-Papuan *Pipistrellus* and *Falsistrellus* (Microchiroptera: Vespertilionidae). *Records of the Western Australian Museum* 12: 435-495
- Kleiman, D.G. (1969). Maternal care, growth rate and development in the noctule (*Nyctalus noctula*), pipistrelle (*Pipistrellus pipistrellus*), and serotine (*Eptesicus serotinus*) bats. *Journal of Zoology, London* 157: 187-211
- Koopman, K.F. (1970). Zoogeography of bats. Pp. 29-50 in Slaughter, B.H. & Walton, D.W. (eds) *About Bats. A Chiropteran Symposium*. Southern Methodist University Press : Dallas
- Koopman, K.F. (1973). Systematics of Indo-Australian pipistrelles. *Periodicum Biologorum* 75: 113-116
- Koopman, K.F. (1975). Bats of the Sudan. *Bulletin of the American Museum Natural History* 154: 355-443
- Koopman, K.F. (1978). The genus *Nysticeius* (Vespertilionidae), with special reference to tropical Australia. Pp. 165-171 in Olembo, R.J., Castelino, J.B. & Mutere, F.A. (eds) *Proceedings of the Fourth International Bat Research Conference*. Kenya Literature Bureau : Nairobi
- Koopman, K.F. (1982). Results of the Archbold Expeditions. No. 109. Bats from eastern Papua and east Papuan Islands. *American Museum Novitates* 2747: 1-34
- Koopman, K.F. (1984a). Taxonomic and distributional notes on tropical Australian bats. *American Museum Novitates* 2778: 1-48

- Krutzsch, P.H. (1955a). Ectoparasites from some species of bats from western North America. *Journal of Mammalogy* 436: 457-458
- Kulzer, E., Nelson, J.E., McKean, J.L. & Mohres, F.P. (1970). Untersuchungen über die Temperaturregulation australischer Fledermäuse (Microchiroptera). *Zeitschrift für Vergleichende Physiologie* 69: 426-451
- Kunz, T.H. (1973). Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy* 54: 14-32
- Kunz, T.H. (1982). Roosting ecology of bats. Pp. 1-55 in Kunz, T.H. (ed.) *Ecology of Bats*. New York: Plenum Press
- Lee, C.S. & McCabe, R. (1986). The Banda-Celebes-Sulu basin: a trapped piece of Cretaceous-Eocene oceanic crust? *Nature* 22: 51-54
- Linnaeus, C. (1758). *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis synonymis, locs.* 10<sup>th</sup> edn Holmiae: Laurentii Salvii Tomus I 824 pp.
- Longmore, R. (ed.) (1986). *Atlas of Elapid Snakes of Australia*. Australian Flora and Fauna Series No. 7. Canberra: Australian Government Publishing Service v 115 pp.
- Lunney, D. & Barker, J. (1986). The occurrence of *Phoniscus papuensis* (Dobson) (Chiroptera: Vespertilionidae) on the south coast of New South Wales. *Australian Mammalogy* 9: 57-58
- Maddock, T.H. (1971). Some mammal remains from caves in the Naracoorte area. *South Australian Naturalist* 46: 24-27
- Maddock, T.H. & McLeod, A. (1974). Polyoestry in the Little Brown Bat, *Eptesicus pumilus* in Central Australia. *South Australian Naturalist* 48: 50-63
- Maddock, T.H. & McLeod, A. N. (1976). Observations on the Little Brown Bat, *Eptesicus pumilus caurinus* Thomas, in the Tennant Creek area of the Northern Territory, Part One: Introduction and breeding biology. *South Australian Naturalist* 50: 42-50
- Maeda, K. (1982). Studies on the classification of *Miniopterus* in Eurasia, Australia and Melanesia. *Honyurui Kagaku (Mammalian Science) Supplement* No. 1: 1-176
- Makin, D. & Mendelssohn, H. (1985). Insectivorous bats victims of Israeli campaign. BATS (BCI Newsletter) 2(4): 1-2
- Marshall, A.G. (1982). Ecology of insects parasitic on bats. Pp. 369-401 in Kunz, T.H. (ed.) *Ecology of Bats*. Plenum Press : New York
- Martin, H. (1984). Australian phytogeography. Pp. 17-30 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Martini, E. (1959). Strutture dell'intracardio negli insettivori e nei chiroterri. *Revista Biologia* 51: 501-15
- Matthes, E. (1934). Geruchsorgan. Pp. 879-948 in Bolk, L. (ed.) *Handbuch der vergleichenden Anatomie der Wirbeltiere*. Berlin: Urban & Schwarzenberg
- McCracken, G.F. & Wilkinson, G.S. (1986). Allozyme techniques and kinship assessment in bats. In Kunz, T.H. (ed.) *Behavioural and Ecological Techniques for Research on Bats*. Washington, D.C.: Smithsonian Press
- McCracken, G.F. & Gelfand, D.L. (1986). Individual variation in the isolation calls of Mexican free-tailed bat pups (*Tadarida brasiliensis mexicana*). *Animal Behaviour* 34: 1078-1086
- McKean, J.L. (1975). The bats of Lord Howe Island with the description of a new nyctophiline bat. *Australian Mammalogy* 1: 329-32
- McKean, J.L. & Hall, L.S. (1964). Notes on Microchiropteran bats. *Victorian Naturalist* 81: 36-37

- McKean, J.L. & Hall, L.S. (1965). Distribution of the large-footed *Myotis*, *Myotis adversus* in Australia. *Victorian Naturalist* 82: 164-168
- McKean, J.L. & Hamilton-Smith, E. (1967). Litter size and maternity sites in Australian bats (Chiroptera). *Victorian Naturalist* 84: 203-206
- McKean, J.L., Richards, G.C. & Price, W.J. (1978). A taxonomic appraisal of *Eptesicus* (Chiroptera: Vespertilionidae) in Australia. *Australian Journal of Zoology* 26: 529-537
- McKenzie, N.L. & Rolfe, J.L. (1986). Structure of insectivorous bat guilds in the Kimberley mangroves in Australia. *Journal of Animal Ecology* 55: 401-420
- Miller, G.S. (1907). The families and genera of bats. *Bulletin of the U.S. National Museum* 57: xvii 282 pp. 14 pls
- Morrison, P. (1959). Body temperatures in some Australian mammals. 1. Chiroptera. *Biological Bulletin, Wood's Hole* 116(3): 484-497
- Nelson, G. & Platnick, N. (1981). *Systematics and Biogeography - Cladistics and Vicariance*. New York: Columbia University Press 567 pp.
- Neuweiler, G. (1984). Foraging, echolocation and audition in bats. *Naturwissenschaften* 71: 446-455
- Nix, H. (1982). Environmental determinants of biogeography and evolution in Terra Australis. Pp. 47-66 in Barker, W.R. & Greenslade, P.J.M. (eds) *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications : Frewville
- Norberg, U.M. (1981). Flight morphology and the ecological niche in some birds and bats. *Proceedings of the Zoological Society of London* 48: 173-197
- O'Neill, M.C. & Taylor, R.J. (1986). Observations on the flight patterns and foraging behaviour of Tasmanian bats. *Wildlife Research* 13: 427-432
- Orr, R.T. (1954). Natural history of the pallid bat, *Antrozous pallidus*. *Proceedings of the California Academy of Science* 28: 165-246
- Orr, R.T. (1970). Development: prenatal and postnatal. Pp. 217-231 in Winsatt, W.A. (ed.) *Biology of Bats. Vol. 1*. New York: Academic Press
- Parnaby, H. (1976). Live records for Victoria of the bat *Pipistrellus tasmaniensis* (Gould, 1858). *Victorian Naturalist* 93: 190-193
- Pearson, O.P., Koford, M.P. & Pearson, A.K. (1952). Reproduction of the lumped-nosed bat (*Corynorhinus rafinesquei*) in California. *Journal of Mammalogy* 33: 273-320
- Peters, W. (1866a). Ferne Mittheilungen zur Kenntniss der Flederthiere, namenlich über Arten des Leidener und Britischen Museums. *Monatsberichte K Preusse Akadamie Wissenschaft zu Berlin* 1866: 672-681
- Pettigrew, J.S., Dreher, B., McCall, M.J., Hopkins, C.S. and Brown, M. (1988). Peak density and distribution of ganglion cells in the retinae of microchiropteran bats: implications for visual acuity. *Behaviour and Evolution* 32: 39-56.
- Phillips, W.R. & Inwards, S.J. (1985). The annual activity and breeding cycles of Gould's Long-eared bat, *Nyctophilus gouldi* (Microchiroptera: Vespertilionidae). *Australian Journal of Zoology* 33: 111-126
- Pianka, E.R. & Schall, J. (1984). Species densities of Australian vertebrates. Pp. 119-124 in Archer, M. & G. Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia*. (Animals in Space & Time). Hesperian Press : Carlisle
- Pierson, E.D., Sarich, V.M., Lowenstein, J.J. & Daniel, M.J. (1982). *Mystacina* is a phyllostomatoid. *Bat Research News* 23: 78



- Pine, R.H., Carter, D.C. & La Val, R.K. (1971). Status of *Bauerus* Van Gelder and its relationships to other nyctophiline bats. *Journal of Mammalogy* 52: 663-669
- Quay, W.B. (1970a). Integument and derivatives. Pp. 1-56 in Wimsatt, W.A. (ed.) *Biology of Bats*. Academic Press : New York Vol. II [38] [40] [41] insert 'a' into 38, 40, 41
- Quay, W.B. (1970b). Peripheral nervous system. Pp. 153-179 in Wimsatt, W.A. (ed.) *Biology of Bats*. Vol.2. Academic Press : New York
- Rasweiler, J.J. (1977). The care and management of bats as laboratory animals. Pp. 519-617 in Wimsatt, W.A. (ed.) *Biology of Bats*. Vol.3. New York: Academic Press
- Richards, G.C. (1983a). Greater Long-eared Bat *Nyctophilus timoriensis*. p. 328 in Strahan, R. (ed.) *The Australian Museum Complete Book of Australian Mammals The National Photographic Index of Australian Wildlife*. Angus & Robertson : Sydney
- Richards, G.C. (1983c). Large-footed Mouse-eared Bat *Myotis adversus*. P. 346 in Strahan, R. (ed.) *The Australian Museum Complete Book of Australian Mammals. The National Photographic Index of Australian Wildlife*. Sydney: Angus & Robertson
- Richards, G.C., Hall, L.S., Helman, P. & Churchill, S.K. (1982). First discovery of a species of the rare tube-nosed insectivorous bat (*Murina*) in Australia. *Australian Mammalogy* 5: 149-151
- Richardson, E.G. (1977). The biology and evolution of the reproductive cycle of *Miniopterus schreibersii* and *M. australis* (Chiroptera: Vespertilionidae). *Journal of Zoology, London* 183: 353-375
- Robson, S.K. (1984). *Myotis adversus* (Chiroptera: Vespertilionidae): Australia's fish-eating bat. *Australian Mammalogy* 7: 51-52
- Rosenbaum, R.M. (1970). Urinary system. Pp. 331-387 in Wimsatt, W.A. (ed.) *Biology of Bats*. Academic Press : New York Vol. I
- Ross, A. (1967). Ecological aspects of the food habits of insectivorous bats. *Proceedings of the Western Foundation for Vertebrate Zoology* 1: 204-263
- Ryan, R.M. (1963a). Life history and ecology of the Australian lesser long-eared bat, *Nyctophilus geoffroyi* (Leach). Unpublished MSc Thesis, University of Melbourne : Melbourne
- Ryan, R.M. (1966). A new and some imperfectly known Australian *Chalinolobus* and the taxonomic status of African *Glauconycteris*. *Journal of Mammalogy* 47: 86-91
- Sales, G.D. & Pye, J.D. (1974). *Ultrasonic Communication by Animals*. London: Chapman & Hall 281 pp.
- Sanborn, C.C. & Nicholson, A.J. (1950). Bats from New Caledonia, the Solomon Islands and the New Hebrides. *Fieldiana, Zoology* 31: 313-338
- Schimoizumi, J. (1959). Studies of the hibernation of bats. *Scientific Reports of Tokyo Kyoiko Daigaku*, Sect. B 9: 1-36
- Sigé, B. (1974). Données nouvelles sur le genre *Stehlinia* (Vespertilionidae: Chiroptera) du Paléogène d'Europe. *Palaeovertebrata* 6: 255-272
- Simmons, J.A. & Stein, R.A. (1980). Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *Journal of Comparative Physiology* 135: 61-84
- Simmons, J.A., Fenton, M.B. & O'Farrell, M.J. (1979). Echolocation and pursuit of prey by bats. *Science* 203: 16-21
- Simpson, G.G. (1961). Historical zoogeography of Australian mammals. *Evolution* 15: 431-447

- Smith, J.D. (1976). Chiropteran evolution. Pp. 49-69 in Baker, D.C., Jones, J.K. & Carter, D.C. (eds) *Biology of bats of the New World family Phyllostomatidae Part I. Special Publications of the Museum Texas Tech University* 10
- Smith, J.D. & Starrett, A. (1979). Morphometric analysis of chiropteran wings. Pp. 229-316 in Baker, R.J., Jones, K.J. & Carter, D.C. (eds) *Biology of bats of the New World family Phyllostomatidae, Part III. Special Publications of the Museum of Texas Tech University* 16: 1-441
- Stebbing, R.E. (1966). A population study of bats of the genus *Plecotus*. *Journal of Zoology, London* 150: 53-75
- Strahan, R. (ed). (1983). *The Australian Museum Complete Book of Australian Mammals*. The National Photographic Index of Australian Wildlife. Angus & Robertson : Sydney xx 530 pp.
- Strong, D.R., Jr., Simberloff, D., Abele, L.G. & Thistle, A.B. (1984). *Ecological Communities: conceptual issues and the evidence*. Princeton: Princeton University Press xiii 613 pp.
- Suthers, R.A. (1970). Vision, olfaction, taste. Pp. 265-309 in Wimsatt, W.A. (ed.) *Biology of Bats. Vol. 2*. Academic Press : New York
- Tate, G.H.H. (1941a). Results of the Archbold Expeditions. No. 39. Review of *Myotis* of Eurasia. *Bulletin of the American Museum Natural History* 78: 537-565
- Tate, G.H.H. (1941b). Results of the Archbold Expeditions. No. 40. Notes on vespertilionid bats of the subfamilies Miniopterinae, Murinae, Kerivoulinae, and Nyctophilinae. *Bulletin of the American Museum of Natural History* 78: 567-597
- Tate, G.H.H. (1942). Results of the Archbold Expeditions. No. 47. Review of the vespertilionine bats with special attention to the genera and species in the Archbold Collection. *Bulletin of the American Museum of Natural History* 80: 221-297
- Tate, G.H.H. (1946). Geographical distribution of bats in the Australian archipelago. *American Museum Novitates* 1323: 1-21
- Taylor, R.J. & O'Neill, M.C. (1986). Composition of the bat communities in Tasmanian forests. *Australian Mammalogy* 9: 125-130
- Thompson, D. & Fenton, M.B. (1982). Echolocation and feeding behaviour of *Myotis adversus* (Chiroptera : Vespertilionidae). *Australian Journal of Zoology* 30: 543-546
- Tidemann, C.R. (1967). Some mammal remains from cave deposits in the southeast of South Australia. *South Australian Naturalist* 42: 21-27
- Tidemann, C.R. (1982). Sex differences in seasonal changes of brown adipose tissue and activity of the Australian vespertilionid bat, *Eptesicus vulturinus*. *Australian Journal of Zoology* 30: 15-22
- Tidemann, C.R. & Woodside, D.P. (1978). A collapsible bat-trap and a comparison of results obtained with the trap and with mist-nets. *Australian Wildlife Research* 5: 355-362
- Tidemann, C.R., Woodside, D.P., Adams, M. & Baverstock, P.R. (1981). Taxonomic separation of *Eptesicus* (Chiroptera: Vespertilionidae) in south-eastern Australia by discriminant analysis and electrophoresis. *Australian Journal of Zoology* 29: 119-128
- Troughton, E. le G. (1920). Notes on Australian mammals. No. I. *Records of the Australian Museum* 13: 118-119
- Troughton, E. le G. (1922). Notes on Australian bats, and the occurrence of *Chalinolobus gouldii*, Gray at Norfolk Island. *Australian Zoologist* 3: 39-41

- Troughton, E. le G. (1941). *Furred Animals of Australia*. Angus & Robertson : Sydney 1<sup>st</sup> edn 374 pp.
- Tuttle, M.D. (1974). An improved trap for bats. *Journal of Mammalogy* 55: 475-477
- Tuttle, M.D. (1975). Population ecology of the Gray Bat (*Myotis grisescens*: factors influencing early growth and development. *Occasional Papers of the Museum of Natural History, University of Kansas* 36: 1-24
- Tuttle, M.D. & Stevenson, D. (1982). Growth and survival of bats. Pp. 105-149 in Kunz, T.H. (ed.) *Ecology of Bats*. New York: Plenum Press
- Van Deusen, H.M. & Koopman, K.F. (1971). Results of the Archbold Expeditions. No. 95. The genus *Chalinolobus* (Chiroptera, Vespertilionidae). Taxonomic review of *Chalinolobus picatus*, *C. nigrogriseus* and *C. rogersi*. *American Museum Novitates* 2468: 1-30
- Van Valen, L. (1979). The evolution of bats. *Evolutionary Theory* 4: 103-121
- Vaughan, T.A. (1959). Functional morphology of three bats, *Eumops*, *Myotis*, *Macrotus*. *Publications of the Museum of Natural History University of Kansas* 1: 1-153
- Vestjens, W.J.M. & Hall, L.S. (1977). Stomach contents of forty-two species of bats from the Australasian region. *Australian Wildlife Research* 4: 25-35
- Wakefield, N.A. (1963a). Mammal sub-fossils from near Portland, Victoria. *Victorian Naturalist* 80: 39-45
- Wakefield, N.A. (1963b). Mammal remains from the Grampians, Victoria. *Victorian Naturalist* 80: 130-133
- Wakefield, N.A. (1964b). Recent mammalian sub-fossils of the basalt plains of Victoria. *Proceedings of the Royal Society of Victoria* 77: 419-426
- Wakefield, N.A. (1967a). Mammal bones in the Buchan district. *Victorian Naturalist* 84: 211 -214
- Walker, E.P. (1964). *Mammals of the World*. Vol. 1.. Baltimore: John Hopkins Press xviii 644 pp.
- Wallace, G.I. (1978). A histological study of the early stage pregnancy in the Bent-winged Bat, *Miniopterus schreibersii* in north-eastern New South Wales (30°27'S). *Journal of Zoology, London* 185: 519-537
- Walton, D.W. & Walton, G.M. (1968). Comparative osteology of the pelvic and pectoral girdle of the Phyllostomatidae (Chiroptera; Mammalia). *Journal of the Graduate Research Center* 37: 1-35
- Walton, D.W. & Walton, G.M. (1970). Post-cranial osteology of bats. Pp. 93-126 in Slaughter, B.H. & Walton, D.W. (eds) *About Bats. A Chiropteran Symposium*. Southern Methodist University Press : Dallas
- Winge, H. (1941). *The Interrelationships of the Mammalian Genera*. [Translated by E. Deichmann & G.M. Allen, edited by Jensen, A.S., Sparck, R. & Volsoe] Kobenhavn: H. Reitzels Forlag Vol. 1 418 pp.
- Woodside, D.P. & Long, A. (1984). Observations on the feeding habits of the Greater Broad-nosed Bat, *Nysticeius rueppelli* (Chiroptera: Vespertilionidae). *Australian Mammalogy* 7: 121-129
- Woodside, D.P. & Taylor, K.J. (1985). Echolocation calls of fourteen bats from eastern New South Wales. *Australian Mammalogy* 8: 279-297
- Woodsworth, G.C., Bell, G.P. & Fenton, M.B. (1981). Observations of the echolocation, feeding behaviour and habitat use of *Euderma maculatum* (Chiroptera: Vespertilionidae) in southeastern British Columbia. *Canadian Journal of Zoology* 59: 1098-1102
- Young, R.A. (1979). Foetal development at birth in the Chocolate Wattled Bat, *Chalinolobus morio* (Vespertilionidae). *Victorian Naturalist* 96: 90-91