



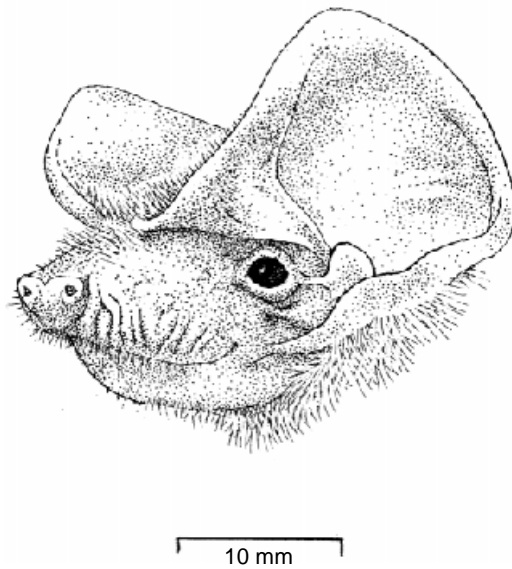
# FAUNA *of* AUSTRALIA

## 43. MOLOSSIDAE

F.R. ALLISON



## DEFINITION AND GENERAL DESCRIPTION



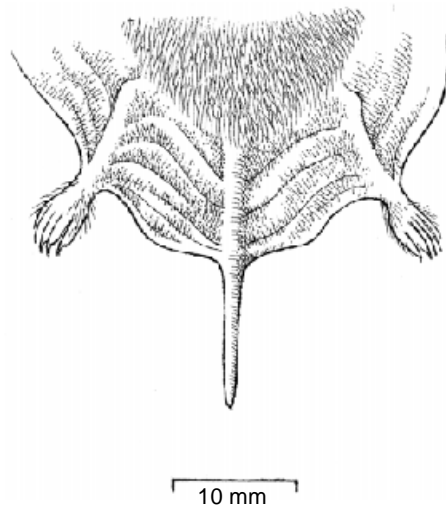
**Figure 43.1** A near lateral view of the head of the Little Mastiff-bat (*Mormopterus planiceps*), a relatively common species of Australian molossid. (© ABRS) [F. Knight]

A molossid bat can be recognised readily by a number of marked peculiarities of the external morphology (Rosevear 1965). The face, has thick-lipped heavy jowls that are often vertically wrinkled or creased (Fig. 43.1). The ears are thick, sometimes pricked (*Mormopterus*), or floppy and folded (*Tadarida*) and may be separated, joined or just meet over the forehead. The small tragus is usually roughly square in outline and there may be minute horny outgrowths on the inner margin of the ear (Rosevear 1965). There are no noseleaves or other fleshy facial appendages and the nostrils, on a small pad, are directed forward. The whole face recalls that of a mastiff, hence the common name of mastiff-bat used for some members of this family. The generic name *Molossus*, the oldest genus and thus the basis for the family name, was the

name of the mastiff-like dogs of shepherds of ancient Greece (Jaeger 1972). The appearance and some of the range of facial features are shown in the illustrations in Rosevear (1965), Peterson & Harrison (1970), Peterson (1972) and Nowak & Paradiso (1983a). The variation that can be exhibited in one genus, *Eumops*, is demonstrated in Eger (1977).

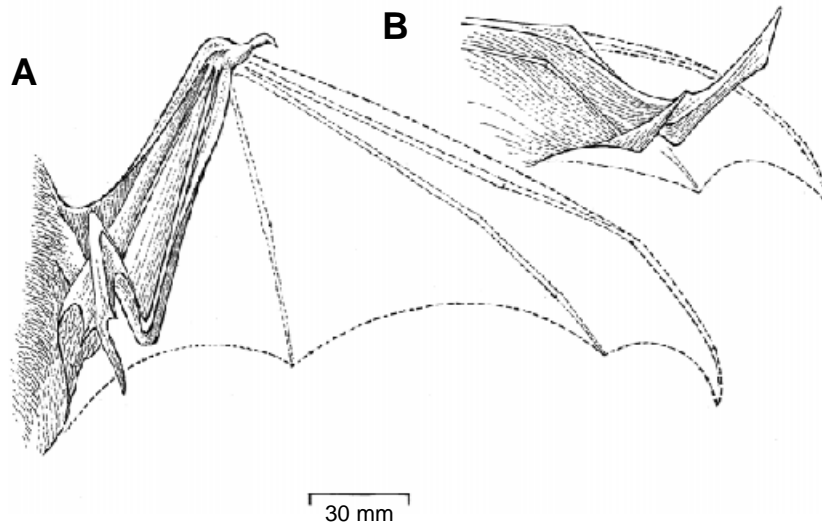
The tail is thickened and extends for half to three-quarters of its length from the edge of the thick, wrinkled uropatagium (Fig. 43.2). A calcar is present, but it is not obvious because of the thickness of the uropatagium. There is no calcarial lobe. The form of the tail has resulted in the name 'free-tailed bats' being used for molossids in all parts of the world except Australia, where this name was applied to the emballonurids by Troughton (1926) and Iredale & Troughton (1934) who referred to Australian molossids as wrinkled-lipped bats.

In contrast with the sheath-tailed bats (*Emballonuridae*) in which the tail protrudes from the upper surface of the tail membrane, and



**Figure 43.2** The tail of a molossid in dorsal aspect showing its general form, the interfemoral membrane and feet. (© ABRS) [F. Knight]





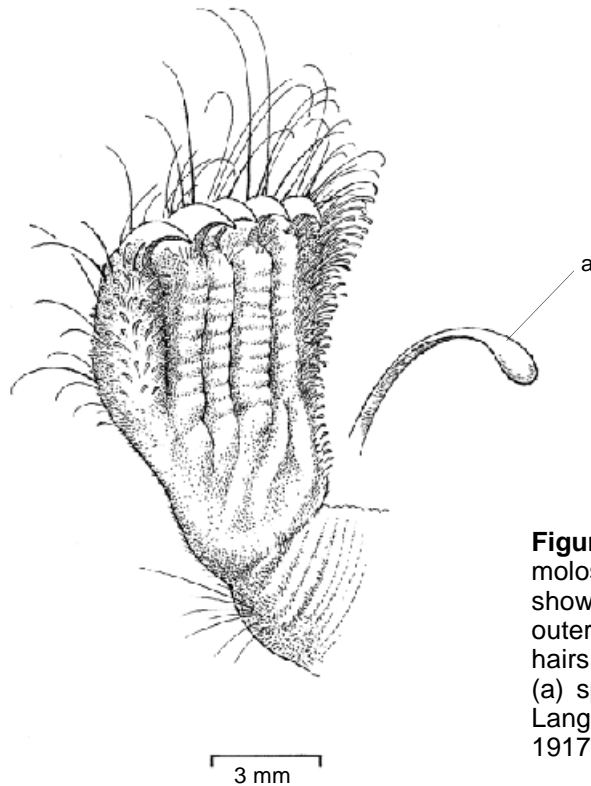
**Figure 43.3** The wing of a molossid bat showing the tip folding mechanism; **A**, ventral view with wing almost completely folded (position of wing when extended shown by dotted lines); **B**, ventral view of the tip of a half open wing. A rotation of the joint (i) between the metacarpal and first phalanx of the third digit is necessary before the wing obtains the flight position. (After Lang & Chapin in Allen *et al.* 1917; © ABRs) [F. Knight]

with the vespertilionid bats (*Vespertilionidae*) and most other microchiropterans where the tail is totally (or almost totally) contained in the tail membrane, the long thin tail of the mouse-tailed bats (*Rhinopomatidae*) lacks a calcar and has only a fifth or sixth of its length in the brief interfemoral membrane.

The extended wing is long and narrow, with a mechanism for folding the tip that rotates at the joint of the metacarpal and first phalanx of the digit III (Fig. 43.3). The wing membranes are thick and leathery with corrugations and hair tracts. The third phalanx of digit III is usually cartilaginous except at the extreme base (Koopman 1984b), although in *Mystacina* (*Mystacinidae*) it is bony. The forearm is more flattened than in other bats (Vaughan & Bateman 1980) and the thumb is short and thick with a swollen base, this morphology being associated with terrestrial locomotion. In Verschuren (1957) this pad is shown on the drawing of the thumb of *Tadarida midas*. Other bats, such as emballonurids and miniopterines, employ different methods of wing-tip folding.

The toes of the foot are all the same length, and especially the outer ones, are thickened and fringed with conspicuous, long, curved, spatulate hairs (Fig. 43.4). The New Zealand shorter-tailed bats (*Mystacinidae*) share the character of a complete fibula in a short stout leg with the *Molossidae*, but differ in a number of other features, such as the taloned claws of thumb and toes. These features emphasise the importance of terrestrial locomotion in the molossids and the significance of the name 'scurrying bats' applied to some species.

Accounts of various scope of the family have been given by Miller (1907), Koopman & Jones (1970), Vaughan (1972), Yalden & Morris (1975), Nowak & Paradiso (1983a), Koopman (1984a, 1984b), Hill & Smith (1984) and Schober (1984).



**Figure 43.4** The right foot of a molossid bat in ventral aspect showing the relatively thickened outer toes and the spatulate hairs on the first and fifth digits; (a) spatulate hair (x 24). (After Lang & Chapin in Allen *et al.* 1917; © ABRS) [F. Knight]

## HISTORY OF DISCOVERY

### Nomenclature

Considering the distinctive peculiarities of the members of the Molossidae, it is puzzling why the family was included for so long within the families Vespertilionidae, Emballonuridae or Noctilionidae. Molossids are morphologically homogeneous and, in the past, species were mistaken for one another and generic distinctions not appreciated.

Some idea of the appearance of these bats and their general uniformity can be obtained from the coloured photographic plates of North American species in Barbour & Davis (1969) or Whitaker (1980) and of the Australian species in Strahan (1983).

The history of the discovery of this family of bats is clouded with confusion that persists to the present. The generic classification of the Molossidae is best described as unstable (Hill 1986). Specimens have been lost and misidentified and the rules of nomenclature misunderstood and misapplied.

Peters (1865) grouped in his Molossi all those bats that are now termed molossids. The first monograph of this group was that of Dobson (1876) which covered 31 species. Even then the group Molossi was considered to be no more than a part of Emballonuridae. Dobson divided the Molossi into three groups, which he called genera, that closely correspond with the subfamilies of Legendre's (1984) classification. Dobson's subgenera more nearly match present day genera, but not precisely.

The first molossid to be technically named was *Vespertilio molossus*, described by Pallas (1766), the description being based on a specimen of uncertain provenance and the illustrations in Buffon & Daubenton (1763). In 1767, Pallas figured the skull of his specimen. Geoffroy established the genus *Molossus* in

1805. The generic name *Molossus* has often been used incorrectly for other molossid genera, for example, for *Tadarida* (or *Nyctinomus*) in *M. australis* Gray 1839; for *Tadarida* (or *Nyctinomus* or *Chaerephon*) in *M. plicatus* Fischer 1829; for *Mormopterus* in *M. norfolkensis* Gray 1839 and for many of the discrete neotropical genera such as *Eumops*, *Molossops*, *Nyctinomops* and *Promops*. The history of the name *Molossus* is based on Miller (1913), Husson (1962) and Carter & Dolan (1978). The date is given as 1914 on the title page of Miller, but 1913 seems to be the date most commonly quoted.

The priority of the name *Tadarida*, created by Rafinesque (1814) for a Sicilian species, was overlooked for a long time and *Nyctinomus*, a name proposed by Geoffroy St Hilaire (1813a), was applied instead. Lyon (1914) resurrected *Tadarida* and incorrectly gave the date of publication of *Nyctinomus* as 1818 (see Mahoney & Walton 1988 for further details).

Dobson (1878) and Miller (1907) used *Nyctinomus*, but de Blainville (1837) and Gray (1866) used *Tadarida*. Others continuing to use *Nyctinomus* were Revilliod (1920) and Tate (1952b). Although Gervais (1856) indicated that *Tadarida* (then containing only the single species, *teniotis*) is characterised by the presence of three pairs of lower incisors, he then described *Nyctinomus brasiliensis*, which also has three pairs of lower incisors. Allen (1939) maintained both names, keeping *Tadarida* for American species and *Nyctinomus* for the Old World species, despite the Old World type localities of both generic names. Engesser (1972), referring a fossil bat to *Tadarida*, used *Nyctinomus* for two species from the Miocene, giving as his reasons the lack of revision of the genus. Freeman (1981b) used *Tadarida* for the Old World forms and for *T. brasiliensis* in the New World, but adopted Miller's *Nyctinomops* for the bats formerly classed as New World *Tadarida*.

Whether *Tadarida* or *Nyctinomus* was used as the generic name, the genus was subdivided into subgenera and treated variously by different workers. In this account, *Tadarida* is regarded as the senior synonym. *Chaerephon* (often misspelled *Chaerophon*) was proposed as a subgenus of *Nyctinomus* by Dobson (1874) and elevated to generic rank by Andersen (1907). The name subsequently has been used at both levels. The latest classification (Legendre 1983) gives *Chaerephon* as a subgenus, but in most other recent literature it is used as a genus (see Freeman 1981b).

Peters (1865) established *Mormopterus* as a subgenus of *Nyctinomus* with the Malagasian type species, *Nyctinomus jugularis*. It was treated as a subgenus of *Tadarida* in Ellerman & Morrison-Scott (1951), Hayman & Hill (1971) and Hill (1983) and as a genus by Freeman (1981b), Honacki, Kinman & Koeppl (1982) and Corbett & Hill (1986).

### Discovery in Australia

A specimen of a molossid bat was presented by Major Macarthur to the United Services Institution and was described by Gray (1838) as *Molossus australis* (Gould 1858). The specimen seems subsequently to have been incorporated into the British Museum (Natural History) collections, as Hill (1961) quotes the registration number BMNH 61.4.1.9 for the type of *M. australis*. Troughton (1967) was of the opinion that the specimen came from near Camden, the New South Wales property of the Macarthur family, but there seems to be no supporting evidence. Gould's account of the species mentions specimens collected by Ludwig Becker from near Melbourne.

Troughton (1926) placed the species in the genus *Nyctinomus*. Iredale & Troughton (1934) proposed the genus *Austronomus* to accommodate it, but this proposal was invalid. This name is now dated as Troughton 1941 and usually accorded subgeneric status. The genus *Tadarida* is now in general use for *australis*, in the subgenus (*Tadarida*) when this category is employed.

Dobson (1878) states that the female of *Tadarida australis* lacked the white band along the flank and the gular pouch of the male. Consequently, when Leche (1884) examined a female bat with a stripe and pouch, he thought it must be a different species, naming it *Nyctinomus albidus*. Jones (1925) investigated this matter and concluded that only one species was involved. *Tadarida australis* is widespread and not uncommon in South Australia (Jones 1925; Aitken 1975). Thomas (1924) described *Nyctinomus australis atratus* from a specimen from Ooldea which lacked the white flank stripe and Tate (1952b) recorded this form from Birdsville. The type of this subspecies (BMNH 24.8.4.8) is considered to be a melanic specimen. Troughton (1967) stated the type to be a youngish female. It is, however, labelled male and, according to Hill (1961), the skull is that of a nearly adult animal. Hall & Richards (1973) reported the species colliding with the blades of wind-driven generators and noted a colour variant with a band of white fur across the ventral surface of the upper thorax. They recorded the species from the Northern Territory. Parker (1973) also recorded the species from the south of the Northern Territory and Thomson (1980) reported it from other localities in the Northern Territory. The bat has been collected in several fauna surveys and is well represented in museums, for example, the Western Australian Museum (Kitchener & Vicker 1981).

McKean & Calaby (1968) described *Tadarida kuboriensis* from New Guinea, which lacks the white flank stripe and is smaller in some measurements when compared with *australis*. Three specimens from New Guinea listed in Hill (1961) as *Tadarida australis atratus* (BMNH 53.207-209) could represent this species. Koopman (1982) considered *T. kuboriensis* to be a subspecies of *T. australis* and Honacki *et al.* (1982) treated it as separate species. The two forms are widely separated geographically.

The next molossid bats discovered in Australia were small species that have been included in the genus *Nyctinomus* by Dobson (1876), Miller (1907) and Troughton (1926), in *Tadarida* by Ride (1970) or in the subgenus (*Mormopterus*) by Tate (1952b), Hill (1961) and Felten (1964); in *Mormopterus* as a genus in Peters (1881) and most recent works including Freeman (1981b), Honacki *et al.* (1982) and Peterson (1985), or in *Micronomus* as a genus by Troughton (1944) or as a subgenus of *Mormopterus* (Laurie & Hill 1954; Legendre 1984). The name *Micronomus*, like *Austronomus*, was invalidly proposed in Iredale & Troughton (1934) and dates from Troughton (1944).

A specimen of molossid bat was purchased by the British Museum from a dealer named Warwick. It has an accession date of 11 October, 1838, determined from its registration number, and is listed with material from Australia, but the locality of origin is given as Norfolk Island. It was named *Molossus norfolkensis* by Gray (1839). Gray (1843) also gave the type locality as Norfolk Island, N.H. in his list of mammals in the British Museum. The description is not a very satisfactory one, being a couplet in a key to the genus *Molossus*. The type specimen, BMNH 38.10.11.56, is still available for study, which is fortunate in view of the poor description and confusion over the species. Troughton (1967) suggested that the specimen was sent by W.S. Macleay to the British Museum from the Sydney district and that it got mixed up with Norfolk Island material. There is no evidence for this assertion from the British Museum registration. The specimen, however, could be from south-eastern Australia, mislabelled as being from Norfolk Island. This species has not been recorded from Norfolk Island, despite searches for it there but similar animals have been collected in south-eastern Australia (Strahan 1980). The account of the species in Troughton (1926) seems to be based on local material and not on the type specimen; the distribution is given as eastern Australia and Norfolk Island. Iredale & Troughton (1934) gave the type locality as Sydney and its distribution as New South Wales and Queensland. This created the erroneous impression that all

small molossid bats from eastern Queensland were referable to *Nyctinomus norfolkensis*. Many of the bats so identified are not of this species. Tate (1952b) misspelled both the generic and specific names in referring some of the small molossid bats from north-eastern Queensland to *Nyctinomys norfolensis*.

Hill (1961) considered *Nyctinomus norfolkensis* a distinct species, different from what he called *N. planiceps*. He included *N. loriae* in *N. planiceps*. Felten (1964) also considered *N. norfolkensis* a distinct species, but thought that the specimen additional to the holotype (listed in Hill 1961 as an example of *norfolkensis*), was not that species, but a specimen of what he called *N. loriae*, a view with which Hill (*in litt.*) concurs. Felten (1964) considered the specimen described by Tate (1952b) as *N. norfolkensis* to be *N. loriae*, regarding *N. loriae* and *N. planiceps* as separate species. A small molossid bat collected in south-eastern Queensland in 1977 had the typical short sinuate skull and longer forearm length of *Nyctinomus norfolkensis* and was identified as this species. Though a male, it lacks a gular pouch, raising the possibility that this structure in the holotype could be an artefact or age/season dependent (McEvoy, McDonald & Searle 1979). Study of the Australian Museum collection of small molossids revealed two specimens from the Sydney area which have the skull and forearm characters of *N. norfolkensis*. Further specimens collected from eastern New South Wales have been identified as that species (Parnaby 1984).

In the course of a fauna survey, small molossid bats collected at Toolom, in north-eastern New South Wales, were referred to *Nyctinomus norfolkensis* (Calaby 1966). Detailed examination at the CSIRO Wildlife Collection at Canberra revealed a single specimen of what is here called *N. planiceps*, while some taken from a tree hollow proved to be *N. norfolkensis*. The suggestion that they could have been hibernating possibly resulted from confusion with their daily torpor. In Australia, molossids do not seem to hibernate and the date of collection is, in any case, inappropriate. These specimens were host to the ischnopsyllid flea *Coorilla longictenis* (Dunnet & Mardon 1973).

*Nyctinomus norfolkensis* is not numerous in museum collections. Apart from the holotype in the British Museum (Natural History), the specimens noted above are in the Australian Museum, the CSIRO Wildlife Collection and the Queensland Museum.

Four names are associated with the next molossid bat recorded from Australia. *Nyctinomus planiceps* was named by Peters (1866b) from material described as ‘ostensibly from Sydney’ and Mertens (1925), in selecting a lectotype, gave the type locality as ‘probably Sydney’. The lectotype and other specimen were females. Whether Peters had available the specimens which had come from Becker in 1860 is not clear. This latter series included males and, in view of the diagnostic character of the absence of gular pouch in the male, it is surprising that a male was not selected as type. Peters (1881) listed *N. planiceps* as a synonym of *N. norfolkensis*.

The second name applied to *Nyctinomus planiceps* was *Molossus wilcoxii* (see Krefft 1873), a *nomen nudum*, and either a synonym of *N. norfolkensis* (Iredale & Troughton 1934; Hill 1961) or of *N. planiceps* (Felten 1964).

The third name is *Nyctinomus petersi* Leche 1884, and is ostensibly based on South Australian material. Since South Australia (in Leche’s usage) also included what is now the Northern Territory, his specimens may actually have come from there. The syntype of *N. petersi* is in the British Museum (Natural History) as BMNH 90.8.1.12 (Hill 1961) and it may be this specimen that Tate (1952b) noted as labelled ‘Adelaide’. Leche distinguished *N. petersi* from *N. norfolkensis* by: the lack of a gular pouch in both sexes; nostrils opening forward instead of sublaterally; the wing membranes attached to the tibia a short distance from, instead of at the ankle; the innerside of the first lower premolar not covered by the cingulum of the second premolar as it is in *norfolkensis*, and,



the presence of only two pairs of deeply bifid incisors in the lower jaw *Nyctinomus norfolkensis* is said to have an additional third outer pair of very small lower incisors. The latter difference may be an individual variation or dependent upon age.

The fourth name applied to *Nyctinomus planiceps* is *N. loriae* Thomas 1897 with type locality Kamali, Papua. The short fur and white wing membranes, outside a line from knee to elbow, distinguish it from *N. norfolkensis*, 'but also from the latter's continental representative *N. wilcoxii* Krefft (*N. planiceps*, Peters)'.

Dobson (1876) amended the name *norfolkensis* to *norfolcensis* (possibly to conform with better classical Latin) and included *planiceps* and *wilcoxii* as synonyms. Jones (1925) recorded a small female molossid from South Australia as *Nyctinonomus petersi*, without giving a locality for the specimen and provided illustrations and measurements. Troughton (1926) listed *Nyctinomus planiceps*, with *N. petersi* as a junior synonym, and included some of the features distinguishing it from *N. norfolkensis* that were given by Leche (1884). Distribution is given as south and south-western Australia which, combined with the Sydney type locality for *norfolkensis*, has tended to inhibit the use of the name *N. planiceps* for bats from eastern Australia. Iredale & Troughton (1934) included *Nyctinomus petersi* as a synonym of *N. planiceps* and altered the type locality of 'probably Sydney' to Western Australia without giving any reason for this change. They erected the genus *Micronomus* to accommodate *N. norfolkensis* (type species) and *N. planiceps*, but this name is invalid and should be referred to as *Micronomus* Troughton 1944, having been validly proposed in the second edition of *Furred Animals of Australia*. Laurie & Hill (1954) considered *Nyctinomus loriae* to be a race of *Tadarida norfolkensis* in the subgenus *Micronomus*.

A small molossid bat from the Cobourg Peninsula, Northern Territory, was named *Tadarida loriae cobourgiana* (see Johnson 1959). Photographs of the skull of this animal are included in Johnson (1964). Hill (1961) regarded *Nyctinomus loriae* and *Tadarida cobourgiana* as subspecies of *N. planiceps*, although Felten (1964) treated *N. planiceps* and *N. loriae* as separate species, the latter with subspecies *cobourgiana* and *ridei*. Both these studies were based on rather limited material. Since the skull height/condylobasal length ratio proposed by Felten (1964) to distinguish *Nyctinomus planiceps* and *N. loriae* was found to be untenable, the name *N. planiceps*, as the prior name, was used for these bats (Winter & Allison 1980), a view endorsed by Koopman (1984a, 1984b). *Nyctinomus planiceps* is perhaps best regarded as a species complex. For certain morphological attributes (such as penis length), individuals appear to fall into discrete size classes and distributions. With other features, such as body size and colour, the picture is less clear. Electrophoretic work may contribute to a better understanding of the *N. planiceps* mosaic.

A small undescribed molossid from central Queensland seems, on cranial characters, not to be a member of the *Nyctinomus planiceps* complex (F.R. Allison unpublished observation)

A study of the small molossid bats from north-eastern Queensland fauna surveys (Lavery & Johnson 1967; 1974; Lavery & Grimes 1974) suggests that the picture presented by the literature was at variance with the actual state of affairs. Neither of the two species collected from the surveyed area were conspecific with *Nyctinomus norfolkensis* and only the smaller of these species could be *N. planiceps* or *N. loriae*. Another name was required for the larger species. Comparison with material of *N. beccarii* in the Australian Museum, a species originally described in Peters (1881) from a specimen from Amboina in the Moluccas, indicated this would be a suitable name to apply. The name *N. beccarii* was adopted independently by a number of people (Hill 1961;

Stephan & Nelson 1981; Honacki *et al.* 1982; Strahan 1983) and the name came into general use without any formal announcement that the species was found in Australia. The status of the Australian form of *N. beccarii* is uncertain (Hill 1983; Koopman 1984a; Peterson 1985). Examination of ‘*Mormopterus*’ in a number of Australian collections revealed *N. beccarii sensu latissimo* to be present not only in Queensland, but also in the Northern Territory (CSIRO Wildlife Collections and Central Australian Wildlife Collection) and in Western Australia (Kitchener & Vicker 1981). The species also is represented in the British Museum (Natural History) and North American collections. To judge by the measurements quoted in Felten (1964), some of the specimens from central Australia and Western Australia represent *N. beccarii*, as are some specimens referred to *Tadarida lorae cobourgiana* by Parker (1973).

In 1905, while staying on Alexandria Station, a property in the Northern Territory, W. Stalker collected a molossid which subsequently was described (Thomas 1906b) as the race *colonicus* of the bat then considered to be *Nyctinomus plicatus* (Buchanan 1800). The type of *N. p. colonicus* is in the British Museum (Natural History) with the registration number BMNH 6.3.9.16. Jones (1925) called this bat *Chaerephon plicatus*, but suggested that further study would show that it was a species in its own right. He gave the name of the describer of *Nyctinomus p. colonicus* as Buchanan-Hamilton and recorded the species from northern parts of South Australia, although there are no recent records from that state. Aitken (1975) gave it as a ‘doubtful inhabitant of S[outh] A[ustralia], but if present in extreme north-east corner only’.

Tate (1952b) recorded specimens collected at Malbon near Cloncurry and at Pentland by Gabriell Neuhauser as *Nyctinomus colonicus*. He compared this species with *N. plicatus* and regarded the former as a distinct species. Although referring to Buchanan Hamilton’s [*sic*] account of ‘*Vespertilio*’ *plicatus*, he attributed the name to *Molossus plicatus* Fisher 1829. Hill (1961) recorded the species as *Tadarida jobensis colonicus*. *Tadarida jobensis* was described by Miller (1902) as *Nyctinomus jobensis* from Japen (Jobe) Island, Dutch New Guinea (now Irian Jaya). The skulls of *T. plicata* and *T. jobensis* are very similar, though there are differences in their external features; this could have contributed to the confusion. Hill (1961) gave reasons for treating *T. jobensis* as a closely related, but distinct, Australian representative of *T. plicata*. Parker (1973) recorded the species *T. jobensis* from the Northern Territory. The species is well represented in museums, for example in the Western Australian Museum (Kitchener & Vicker 1981).

## MORPHOLOGY AND PHYSIOLOGY

Some details of the morphology of Molossids, especially that of the skeleton and teeth, have long been known (Miller 1907). However, details of soft parts are not so well characterised. There are logistic problems in studying small flying animals that are difficult to keep in captivity. Monitoring aspects of their physiology is especially difficult when the animals are unrestrained.

Molossid bats are frequently cited as examples by authors in the three volume series on the biology of bats edited by Wimsatt (1970–1977) and in the proceedings of a symposium on bat biology edited by Slaughter & Walton (1970). Matters relevant to molossid bats are mentioned in a series of publications on the biology of phyllostomid bats (Baker, Jones & Carter 1976–1979) and in proceedings of conferences on bat research (Olembo, Castelino & Mutere 1978; Wilson & Gardner 1980). Much of the work done on the family has been carried out on New World taxa, especially the readily available Brazilian Free-tailed Bat (*Tadarida brasiliensis*). Studies of this species have received impetus from concern over the marked decline in its numbers suspected as being caused by pesticides, and by its role in the spread of rabies to

people. Information on this much-studied species has been quoted to provide a guide to parameters on molossid biology when data from Australian species are not available.

### External Characteristics

Size range: A number of measurements can be used to express the size range in bats, such as total length, head and body length, skull length, forearm length and weight. Depending on the character chosen, the sequence in which molossid species appear on a size scale varies, even though the design of all molossids is so similar. Weight, which would seem to be the best expression of size, is variable in bats, depending on such factors as sex, fat storage and stage of pregnancy (Table 43.1).

**Table 43.1** Ranges of body measurements in the Molossidae.

CHARACTER	RANGE	RATIO min : max
Total length (TL)	68–170 mm	1:2.5
head and body (HB)	40–130 mm	1:3.2
Greatest skull length (GSL)	13.2–30.4 mm	1:2.3
Forearm (FA)	28.6–74.6 mm	1:2.6
Weight (Wt)	5–196 g	1:3.4

Apart from those factors which influence the size of all animals, such as thermoregulation, bats are also restrained by aerodynamic considerations. Examination of the size distribution of molossid species indicates that there is a minimum practicable size for the molossid configuration. Smaller bats occur in other families, but these have lower aspect ratio wings and lower wing loadings.

### Body Wall

The fur of molossids is generally short and of a velvety texture. It has been compared with the fur of some fossorial mammals and may be associated with roosting in crevices. Hairs with a spatulate tip are found on the upper lip and on the feet. The function of these hairs has often been debated and is discussed below. The hair on the wing membranes plays an important role in flight and seems to provide some protection to the folded wing membrane and digits from abrasion on roost walls. The cuticular structure of the hair is characteristic (Benedict 1957; Miles 1965). In Brazilian Free-tailed Bats there is a single annual moult; in males this occurs mostly in July and in females in August (in the Northern Hemisphere; Constantine 1957; Barbour & Davis 1969).

### Skeletal System

Molossid skulls are generally broad and flattened, whereas those of *Cheiromeles*, *Molossus*, *Promops* and some *Mops*, are quite deep. The skulls of some genera/subgenera/species are much flattened in profile, consistent with crevice-dwelling. Examples include the Little Mastiff-bat (*Mormopterus planiceps*), *M. (Platymops) setiger*, *M. (Sauromys) petrophilus* and *Neoplatymops mattogrossensis* (Peterson 1965). Some species have a prominent sagittal crest and all have a marked lambdoidal crest. The skulls of most species are illustrated in Freeman (1981b). Drawings of skulls representative of different genera are shown in Miller (1907) and the skulls of Australian bats in Jones (1925) and Felten (1964). The specimen used as the model for the Eastern

Little Mastiff-bat (*Mormopterus norfolkensis*) in Freeman (1981b) is identified as *M. planiceps* in Koopman (1984a). The skull of the Eastern Little Mastiff-bat has a more sinuate, less flattened profile, as exemplified by the holotype.

The dental formulae of the family are: I 1/1-3 C 1/1 PM 1 or 2/2 M 3/3 = 26, 28 or 30. The lowest numbers are recorded in *Cheiromeles*, *Molossus*, *Molossops* and *Myopterus*. The genera differ in the numbers of lower incisors and upper premolars and in the structure of the M<sub>3</sub>. The Australian genera have the formulae: I 1/2 C 1/1 PM 1-2/2 M 3/3 = 28 or 30.

The vertebral column is made up of seven cervicals, 13 thoracics with ribs, six lumbar, four or five sacral and 10 or 11 caudal vertebrae. The last cervical vertebra is fused with the first thoracic and the lumbar vertebrae are not ankylosed (Miller 1907; Walton & Walton 1970). The shoulder girdle is in some respects very advanced with complete double articulation of the humerus and scapula, and with the surface on which the trochiter (or greater tuberosity) acts, nearly as large as the glenoid fossa. Otherwise it has only minor modifications, such as the thickening of the first rib, fusion of the last cervical and first thoracic vertebrae and a poorly developed mesosternal keel. The trochin (or lesser tuberosity) is much smaller than the trochiter. The structure of the pectoral girdle and its action in molossids is discussed in detail and illustrated in Miller (1907), Vaughan (1970a, 1970b), Walton & Walton (1970), Hill & Smith (1984) and Koopman (1984b). The scapula is broader and better faceted for muscle attachment when compared with most other bats, and there is a large cartilaginous extension at its posterior end. The coracoid process is directed medially instead of laterally (as in other bats), allowing for more efficient muscle use. Distally, the humerus has a locking mechanism with the radius in the form of a spinous process on the medial epicondyle. The ulna provides an extended bearing surface for the articulation with the humerus. These characteristic features are highly developed in the Molossidae.

The metacarpals are slender, cylindrical bones expanded distally at the articulation with the phalanges and conform with the general pattern of length 3-4-5-2-1 (longest to shortest). The first digit has two phalanges with a claw. Digit II has one phalanx and digits III-V each have three phalanges, though the third phalanx of digits IV and V is cartilaginous and not very obvious; it may not represent a true phalanx. The long narrow wing shape in molossids is indicated by the values of about 2:1 for the ratios Digit III : Digit V and Digit III : Radius; other bats have lower ratios. The first phalanx of digits III and IV flexes posteriorly and the second phalanx anteriorly, so that the wing tip forms a compact bundle not projecting beyond the distal end of the third metacarpal and proximal end of the radius. The pelvic girdle is flattened and the hind limb capable of extensive movement associated with crevice-dwelling and an exceptional crawling ability. The pelvis of *Molossus pretiosus* is illustrated in Miller (1907). The acetabulum is large, as is the head of the femur; the spherical form of the latter head allows a very great freedom of movement. The tibia, with its strong complete fibula and calcar, is shown in Miller (1907). The feet of molossids are short and broad, the hallux has two phalanges, and the remaining digits have three.

The muscular system of microchiropteran bats is described in detail in Vaughan (1970a) with the molossid, *Eumops perotis*, included as an example. The muscles that are unique to the Molossidae, or those relatively better developed in molossids than in other bats, are generally involved with control of the wing surfaces. In bats with specialised flight, these muscles are important for the folding of the wing to assist terrestrial locomotion and its unfolding for flight or with movement on the ground. The difference in the sizes of the two parts of the biceps brachi in molossids and other bats, for example, is reflected in differences in the angle of the coracoid process to the scapula noted above. Foehring & Hermanson (1984) showed that the main flight muscles are composed of fast



oxidative fibres (FO), with some slow oxidative fibres (SO) in accessory flight muscles in Brazilian Free-tailed Bats, reflecting the metabolic demands of high-speed flight for extended periods and the requirement to maintain tone within these muscles.

### Locomotion

The flight of molossids is so distinctive that the group is afforded special mention whenever bat flight is discussed (Vaughan, 1970c, 1970d; Smith & Starrett, 1979). The prior view that molossid bats were restricted to rapid straight flight has been modified by observations on feeding Brazilian Free-tailed Bats and *Tadarida macrotis*. Manoeuvres such as ‘flying on irregular paths, fluttering or partially hovering quite abruptly, capturing insects in their flight membranes and immediately flying on in search of more prey’, observed by Simmons *et al.* (1978), run contrary to previous observations. Molossids are apparently capable of two quite distinct flying styles: a fast direct flight when travelling and a slower, more dexterous flight when feeding. During direct flights, the high aspect ratio, high wing loading and a wing camber (with resultant high stalling speed) means that execution of tight, small radius turns is not possible because the upper speed limit dictated by such turns would be below the stalling speed. The slower flight for feeding seems to involve a different wing geometry and silhouette that lowers the stalling speed and thus permits greater manoeuvrability. This is possibly achieved by reducing the aspect ratio and by mechanisms to maintain lift at slow speeds, such as the hair tracts mentioned in Vaughan & Bateman (1980). In confined spaces, most molossids are diffident fliers with flapping wings.

The wing beats at 10–15 Hz in the Brazilian Free-tailed Bat. The speed of flight is 4–10 m/sec (14.4–36 km/h) (Brandon 1979, quoted by Foehring & Hermanson 1984). Davis, Herreid & Short (1962), however, gave speeds of 65–95 km/h. Molossids have been observed at altitudes of up to 3000 m above sea level (Williams, Ireland & Williams 1973) and feeding at 100–300 m above the ground (Simmons *et al.* 1978; Fenton 1982a, 1982b). They descend to near ground level to drink in flight from water surfaces.

Some molossids are capable of taking off from a level surface without difficulty, whilst others need to drop in order to get sufficient air flow over the wing for lift.

On the ground, molossids are able to run about much more rapidly than most bats because of their short strong legs with efficient musculature and their ability to fold their wing tips so they do not protrude. They use the pad at the base of the thumb to support the forelimb. Novick & Leen (1969) depicted the stance employed by these bats when on the ground.

Molossids do not hang up, but cling with all four limbs to the substratum (Kingdon 1974). They demonstrate thigmotaxis and press into crevices and corners to make close contact with the walls, bunching together when in groups. A number of tactile sensory systems that measure both head room and lateral space, assist their occupation of confined roosts. The former group probably entails use of the ‘pimples’ on the outer edge of the ear, lengthened guard hairs on the rump (as with *Eumops underwoodi*) and the ability to unfold the wing tip to detect roof height (for example, *Platymops*: Kingdon 1974). To direct reversing into confined spaces, such bats have the tail free (although lacking the hairs of the emballonurid tail) and possibly the spoon hairs on the outer toes. Most molossids roost in crevices in either rocks or trees. Some will live in buildings and a few species have large colonies in caves. The record of Northern Mastiff-bats (*Chaerephon jobensis*) from a 500 mm long by 50 mm wide crack in an overhang 20 m wide and 14 m deep suggests that this species could enter caves (Begg & McKean 1982). Some species that inhabit narrow cracks in

rocks, such as those of *Sauromys* species and *Neoplatymops* species have, in addition to flat heads and bodies, numerous wart-like structures on their forearms which seem to be correlated to their roosting site preferences.

### Feeding and Digestive System

All molossids feed on arthropods, usually taken in flight. In uncluttered air space, those species that have been studied hunt using narrow band, short, constant frequency (CF) signals of 10–50 kHz without a frequency modulated (FM) component during the search phase. When they have detected and are pursuing prey, they drop the CF signal and introduce an FM component with a single harmonic. In the final closing with the prey, the frequency is lowered and the band width widened. The frequency of signals and whether these are CF or shallow FM are not clear because of Doppler shifts. Simmons *et al.* (1978) made their observations on Brazilian Free-tailed Bats and Big Free-tailed Bats (*Nyctinomops macrotis*) feeding at altitudes of several metres to over 25 m above the ground and with a search frequency of 50 kHz and 40 kHz, respectively. *Tadarida teniotis* used similar sound types when flying above ‘street light level’ and a frequency range of 9–15 kHz. The Australian White-striped Mastiff-bat (*T. australis*) has a similar repertoire and, again at about ‘street light level’, uses frequencies of 10.5–15 kHz (Guppy 1983). Both the latter two species have an audible component to their echolocation calls which has been compared to cricket sounds by Zbinden & Zingg (1986). The ear length of Australian molossids has been shown to match the wavelength for optimum sensitivity. In cluttered or confined situations, a multiple harmonic with several overlapping harmonics is used (Simmons *et al.* 1978).

Observations on flying molossids suggest that they can adjust their wing geometry and become capable of lower flying speeds with greater manoeuvrability. The greater the range at which prey is detected, the greater the opportunity for computing an intercept course to limit the rate of change of direction needed. The range at which insects are first picked up is 4–15 m (Zbinden & Zingg 1986) and the theoretical maximum echolocation range for a molossid is given as 7–100 m (Suthers 1970).

The difficulty of accurately aligning a food item with the mouth and determining when to close the jaws using echolocation is surmounted by having a wide gape and a fringe of hairs around the mouth which, when touched by the prey, trigger its closing. Figures which illustrate these features are found in Allen (1939), Villa-R. (1966) and Freeman (1981a). The wrinkled lips of molossids may facilitate a wide gape and allow for manipulating insect prey, so that it is swallowed head first and the wings and legs sheared off by the chewing/swallowing process. This procedure has been described for *Myotis grisescens* (Vespertilionidae) by Brack & Mumford (1983). The molars triturate food into small particles so efficiently by the shearing action of the interlocking W-shaped crests that identification of ingested prey items is not easy. A gut passage time of 15 minutes has been recorded.

### Circulatory System

The circulatory system is similar to that of other microchiropterans; the heart is about three times the size of that of a laboratory mouse in relative terms. Kallen (1977) gave the heart weight of *Molossus bondae* as 1.2% of body weight, and heart rates of *Eumops perotis* at different temperatures as: 482 at 5 °C, 194 at 30 °C (thermal neutrality) and 257 at 37 °C, respectively.

## Respiration

Little is known about molossid respiration. A feature of molossid cave roosts is the concentration of ammoniacal fumes, often above the level of human tolerance, as well as high concentrations of carbon dioxide. How the bats are able to cope with this gaseous environment is not clear. Cramped, poorly ventilated crevices could develop similar conditions. A synchrony of wing beats with the breathing cycle has been demonstrated for the two microchiropteran species studied in this regard and this is possibly the case in all bats, including molossids. In the cases examined, inspiration takes place during the down beat of the wing cycle (Thomas 1980).

## Excretion

Brazilian Free-tailed Bats, a desert form, have a urine concentration of 3890 mosmol/kg and that of Big Free-tailed Bats collected in mesic habitats, a concentration of 3110 mosmol/kg; the ratio of thicknesses of cortex and medulla were estimated from kidney structure. *Sauromys* species can maintain weight on a diet of insects with no access to free water (Rosenbaum 1970; Gelusco 1980).

## Sense Organs and Nervous System

The brain of Beccari's Mastiff-bat (*Mormopterus beccarii*) is illustrated in Stephan & Nelson (1981). This species has an encephalisation index (EI) of 84, the lowest value for any Australian bat so far examined. The EI for the 18 molossid species studied range from 84 to 130 (compared with a reference line of 100, the mean for vespertilionids). The lower EI values of insectivorous bats compared with frugivorous ones is expected in view of the greater coordination required for hunting insects by echolocation.

The sensory systems of bats are discussed in Henson (1970b) as regards hearing and in Suthers (1970) for vision, olfaction and taste.

Little information is available on vision in molossids. Even a crude system should be able to distinguish clear and obstructed horizons and so indicate direction of open space for flying or detecting obstructions to climb for getting height for take-off when animals are grounded.

Molossids have a persistent, musky ammoniacal smell which makes roosts easy to locate. In such odoriferous animals, olfaction must play a role in their lives, even if it is not employed for active signalling. It appears that they do use odour for communication. The vomeronasal organ is rudimentary in *Tadarida mexicana* (*Rhizomops brasiliensis*) or absent (*Molossus molossus*) and nasopalatine ducts are absent from both species (Bhatnagar 1980).

The basisphenoid pits found in emballonurids and vespertilionids also occur in molossids. A general correlation appears to exist between development of the pits and the size and complexity of the external morphology of the ears. Small, simple-eared bats have the least developed pits and bats with a larger, complex external morphology of the ears, the most developed pits. Basisphenoid pits may function as resonating chambers for sound waves emitted by the larynx, but research is needed to determine their importance in the sonar system. A detailed morphological study has been made of the structure in *Otomops martiensseni* (Valdivieso, Peterson & Tamsitt 1979).

## Endocrine and Exocrine Systems

Endocrine glands. A gland consisting of brown adipose tissue, located under the skin between the shoulder blades, is probably associated with recovery from torpor.

Exocrine glands. The exocrine glands of molossids are probably responsible for their strong smell. The most obvious is the gular gland, found in several genera (such as *Molossus*, *Promops*, *Eumops*, *Otomops*, *Tadarida sensu stricto*, *Platymops* and *Cheiromeles*). The structure of this gland in *Otomops* is described (Harrison 1957). Several molossids have elongated hairs on the crown of the head which are believed to function in scent dispersion. These hairs are associated with a gland which is present in other molossids that do not have such long hairs (Fenton 1985). Werner (1966) distinguished two forms of the Brazilian Free-tailed Bat on the presence and absence of facial sweat glands. *Tadarida (Chaerephon) bemmeleni* has glands beside the root of the tail (Kingdon 1974). Spoon hairs on the face and feet may have glandular or sensory functions. The only Australian molossid with a gular gland, found in both sexes, is the White-striped Mastiff-bat (Jones 1925). The occurrence of gular glands in the Eastern Little Mastiff-bat and other Australian *Mormopterus* species seems doubtful (Koopman 1984a).

### Reproduction

Breeding strategies of molossids have been summarised by Krutzsch & Crichton (1985). Molossids have a wide latitudinal breeding range from 45°N to 45°S. They are essentially monotocous, although twins have been recorded (Krutzsch 1955b). The occurrence of one, two or more annual breeding cycles may be linked not only with latitude, but also with the number of climatic cycles at a locality. Temperate species undergo a single annual reproductive cycle with insemination in early spring (August–October in Southern Hemisphere), with young born in early summer (December–January). The birth of young at one locality takes place over a short time period. Tropical species in the Old World have one or more breeding seasons a year but all Australian species seem to have only one breeding season. Some African species are monoestrous at one location and polyoestrous at another. Although *Molossus molossus* and *M. ater* have two breeding seasons per year, individual females have only one annual reproductive interlude (Haussler, Moller & Schmidt 1981). *Molossus fortis* also is presumed to have two pregnancies per year, but whether any females participate in more than one episode is not known (Krutzsch & Crichton 1985).

The female reproductive system shows a marked asymmetry; only the right ovary and uterine horn of the bicornuate uterus are functional. The female genitalia and reproductive cycle are described and illustrated in Kitchener & Hudson (1982), Krutzsch & Crichton (1985) and Crichton & Krutzsch (1987). The right uterine horn is larger than the left, except in some non-parous females. A corpus luteum develops in the right ovary and degenerates at the time of parturition.

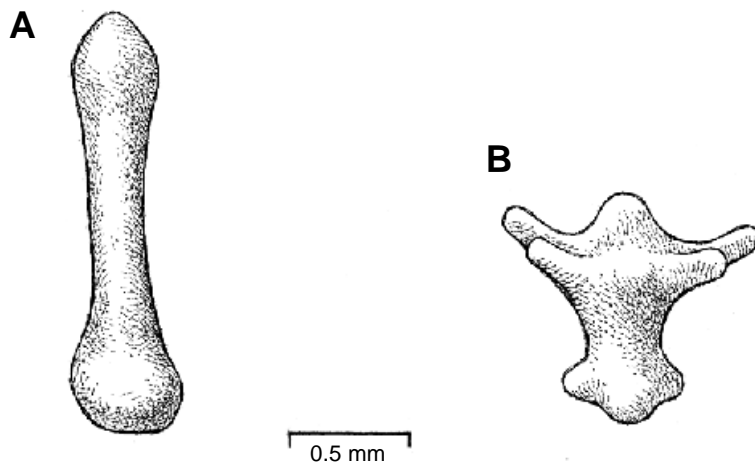
Copulation, ovulation and fertilisation in the White-striped Mastiff-bat, occur around late August. Apparently most females, including young of the year, become pregnant each year and give birth to a single young, usually between mid-December and late January, although occasionally as late as the end of February. This indicates a gestation period of about 14 weeks or more (Kitchener & Hudson 1982).

In one form of the Little Mastiff-bat, copulation occurred in March in Victoria (Holsworth 1986), which coincided with the spermatogenic cycle having commenced in spring (September–October) and epididymal sperm reserves (Krutzsch & Crichton 1987). The species appears to undergo a single pregnancy each year and is monotocous, with conception occurring during late winter/early spring. The timing of events are difficult to reconcile as early embryonic stages up to implantation appeared to span several months (late July/August/September), as did parturition (December/January). Females examined in April



and early May showed no signs of insemination or ovulation despite observed copulation in March. Specialisation of glands in males and females and sperm storage in both sexes are features of this species (Crichton & Krutzsch 1987).

The male reproductive system of molossids is of the usual microchiropteran pattern and is illustrated in Krutzsch & Crichton (1987). The structure of the penis is discussed by Smith & Madkour (1980). Some species have bacula (Brown 1967). The White-striped Mastiff-bat has an unusual trifid baculum (Fig. 43.5) and Beccari's Mastiff-bat and the forms of the Little Mastiff-bat have a rod-like baculum with a slightly spatulate tip. The baculum is shorter and heavier in Beccari's Mastiff-bat (average length 1.71 mm) and in the short and long penis forms of the Little Mastiff-bat the average length is 2.3 mm and 7.9 mm, respectively (F.R. Allison personal observation; Krutzsch & Crichton 1987). Females of some molossid species have os clitoridis (Brown 1967), such a structure is recorded in one form of the Little Mastiff-bat (Crichton & Krutzsch 1987).



**Figure 43.5** The bacula of **A**, *Mormopterus beccarii* and **B**, *Tadarida australis*, which is a very unusual shape. (© ABRS) [F. Knight]

The sperm structure in some Australian molossids has been described. The Little, Northern and White-striped Mastiff-bats have 'blisters' on the acrosome which have been recorded from other bats and may be a feature common to all molossids (Breed & Leigh 1985). Gestation periods for molossid bats are variable: 3.5 months for *Molossus fortis* (Krutzsch & Crichton 1985), 77–84 days in Brazilian Free-tailed Bats in Florida and 100 days for the same species in California (Barbour & Davis 1969). One postulate is that the length of gestation in molossids may be influenced by the temperature in the roost. The development of the preplacenta and placenta in *Tadarida* differs from the pattern seen in all other bats, a condition that may also occur in other molossids (Luckett 1980).

### Embryology and Development

At full term the embryo has a crown-rump length of 25 and 35 mm in species with adult forearm lengths of 36–46 and 65–77 mm, respectively (Barbour & Davis 1969). The young are born pink in colour and turn grey as the fur grows. They are born with their eyes open or soon opening (Kulzer 1962) and have the short wings and large feet found in other young bats. Although not carried, they have the recurved deciduous dentition of young bats that are carried by their mothers. Young are creched in colonial species, but whether the less gregarious species do this is not known. Females have a pair of pectoral mammae. The

young in crèches were thought to be suckled indiscriminately by the mothers of the colony, but it now seems that they exercise some selection in the young they feed: 83% of the mothers nurse young that genetically could have been theirs (Fenton 1985). Studies have been conducted to determine the clues used in recognising young (Gustin 1984; McCracken 1984). The recognition of young molossids by their mothers by olfaction and vocalisations is noted by Fenton (1985). It has been estimated that young Brazilian Free-tailed Bats can fly at about 5 weeks of age.

## NATURAL HISTORY

### Life History

Molossids are nocturnal aerial insectivores, dwelling in crevices, perhaps becoming torpid during the day. They have one or more breeding cycles a year. Some are migratory, but none are known to hibernate, though activity may be reduced during cold spells. Little information is available about their social organisation, sexual segregation and maternity colonies. A number of social patterns has been recorded for molossids: sexual segregation at parturition, sexes mixed at other times; year-round harems; and species without overt sexual segregation at parturition, but with insufficient data to place in other categories (Bradbury 1977b). Because of possible different migration patterns between the sexes and segregated roosting, together with lack of reliable techniques for age determination, demographic data are not available for some species and others have not been studied at all. There are estimates of 25% preadult mortality and more than half the adult females being at least 10 years of age (Davis *et al.* 1962). Males may attain sexual maturity at 16–22 months and females at 9 months (Sherman 1937; Short 1961). The maximum known female lifespan of 7.2 years was recorded for the Brazilian Free-tailed Bat (Cockrum 1973; Tuttle & Stevenson 1982).

### Ecology

One of the first studies which collected information on bat ecology was the American Museum Congo expedition, conducted in what is now Zaire (Allen, Lang & Chapin 1917). Several molossid species were studied and their habits recorded. A later study in the same area continued this work, categorised roosting habits and sites and extended knowledge of African molossids. Because the Molossidae is such a widespread family, its members find mention in many faunal works; often with an extensive account of their ecology and habits. Regional studies have been made in West Africa (Rosevear 1965), East Africa (Kingdon 1974), Arabia (Harrison 1964), Pakistan (Roberts 1977), Mexico (Villa-R. 1966) and Surinam (Husson 1962).

Freeman (1981a) suggested that molossids are divisible into those with heavy dentaries which feed on hard-cased beetles (Coleoptera) and those with weaker dentaries which feed on moths. This distinction is, however, not clear-cut. Whilst it would seem that beetles would be more readily available in the open spaces preferred for hunting by molossids, the bats also take moths. The latter, with their generally weaker fluttering flight (except the hawk moths), are found in more sheltered situations. The capture of moths around street lamps by White-striped Mastiff-bats would seem a good example of where the former occur in a relatively open situation. The clear, but sheltered, flyways provided by tree-lined rivers and roads are other possible feeding sites for molossids preying on moths. The wide range of insect orders taken by molossids (Vestjens & Hall 1977; Whitaker & Mumford 1978) and the lack of knowledge of the distribution and stratification of insects in the night sky prevent reasonable

speculation about the foraging behaviours of these bats. The importance of Hemiptera in molossid diets seems to have been ignored. Available information on the insects taken by Australian molossids are presented by Vestjens & Hall (1977).

Molossids occupy a wide range of habitats from closed forest to desert. They require clear areas in which to hunt and so are generally commoner in open country. They also occur in closed forest (Kingdon 1978), using the space provided by gaps between trees and below the crowns. They can also fly over the canopy, along the forest edge, or along rivers and roadways. Australian molossids have been recorded from habitats of closed forest to desert. The habitat must supply roosting sites which may be buildings, hollow trees or rock crevices in rocky outcrops, river banks or even under stones.

Water usually means open spaces and insect hatches for feeding, but some desert dwelling African molossids are independent of free water.

Potential competitors for the molossid niche of crevice-dwelling nocturnal aerial insectivores are birds and other bats. Most insectivorous birds are diurnal and so probably hunt a different range of (day-)flying insects. Whether dark-adapted swifts feed at night and use their echolocation capability only in roosting and nesting in caves is uncertain (Fenton 1975). The partitioning of resources with other bats seems to depend on the molossids hunting in open spaces at height, whilst other bats hunt lower down, in cover. The suggestion has been made that competition with either swifts or with emballonurids is the reason for the apparently impoverished representation of the Molossidae in the Australian bat fauna (Krzanowski 1984). A more realistic comparison would be numbers of individuals or biomasses rather than numbers of species, but these figures are not available. The fact that Australia represents an outlier of molossid radiation seems to have been ignored.

Molossids eat ants. Stomach contents of the Little Mastiff-bat and *T. loriae* (= *planiceps*) include winged and wingless ants such as *Iridomyrex* or meat ants (Vestjens & Hall 1977). Ants eat molossids. Whitaker & Mumford (1978) recorded a *Tadarida pumila* in Kenya with the heads of 21 ants attached to various parts of its body. In Australia, meat ants have been observed carrying freshly dead, partially eaten, newborn molossids (F.R. Allison unpublished observation). Carnivorous insects in roosts are a threat to young bats.

The study of parasites and diseases of bats is a comparatively neglected field. The problems of identifying pathogens or parasites are compounded by the necessity of matching these with properly identified hosts to provide useful data.

Constantine (1970) concentrated on the human health aspects of disease in bats. He gave examples of bacterial, mycotic, protozoan, rickettsial and viral diseases, some of which are found in molossids. The Brazilian Free-tailed Bat is noted as having been experimentally infected with a number of pathogens. Arboviruses have been isolated from African molossids.

One of the 30 (out of a total of 40) species of North American microchiroptera in which rabies has been recorded is the Brazilian Free-tailed Bat, thus drawing adverse attention to this species, particularly because of its fame as a tourist attraction. Greenhall (1982) pointed out that in the 26 years to that time there were eight deaths in the United States attributable to bites from rabid bats and two from non-bite aerosol transmission. Tuttle (1979) noted: 'Far more people die every year from dog attacks, bee stings, power mower accidents or even from being struck by lightning'. The risk of rabies entering Australia through the agency of bats is virtually negligible. The subject of rabies is dealt with at length in Constantine (1970), Greenhall (1982) and Fenton (1983).

Endoparasite records for molossid bats are not well documented. Groups represented in molossids include trematodes, nematodes and cestodes. Trematodes have been recorded from bats of all zoogeographic regions except Australia. A classification of the genera of nematodes occurring in bats is given in Ubelaker (1970), three genera from the Family Strongylacanthidae are recorded from molossids. The ectoparasitic arthropods found on New World molossids are listed by Webb & Loomis (1977) and include some seventeen groups. Members of the Nycteribiidae (wingless batflies), which are found on most other bats, are absent from or occur only as stragglers on molossids. The reasons for this are not quite clear and may relate to fur texture or roosting site.

Streblids (winged batflies) are recorded from molossids only as stragglers in the Old World. The Old World streblids are found on bats living in roomy caves, suggesting that the roosting sites of molossids might be unfavourable for these parasites. In the New World, one species, *Trichobius joblingi*, is a straggler found on molossids from other bats roosting nearby, but *T. dunni* seems to be host specific to *Molossus bondae*. Other related streblids known to occur on *Molossus* remain to be described (Wenzel, Tipton & Kiewlicz 1966). There are no Australian records of batflies from molossid bats.

Ectoparasitic insects most frequently found on molossids are fleas of the family Ischnopsyllidae, which are restricted to bats. The family contains some 21 genera, 10 of which are found on molossids. Of these, only three, *Porribius*, *Coorilla* and *Lagaropsylla*, are recorded from Australia. The host specificity and distribution of these genera are interesting. The genus *Porribius* has two species in Australia and is polyxenous, having been found on White-striped Mastiff-bats and vespertilionids. Whereas *P. bathyllus* is equally well documented from White-striped Mastiff-bats and vespertilionids, there is only one record of *P. caminae* from White-striped Mastiff-bats and about 24 from vespertilionids. *Porribius papuanus* is recorded from an unidentified New Guinean bat. *Porribius pacificus* from New Zealand, where there are no molossids, is recorded from *Chalinolobus tuberculatus* and *Mystacina tuberculata*. The genus also occurs in Tasmania where there are no molossids, so its presence on White-striped Mastiff-bats could be due to the sharing of roosting sites with other bats.

Of the genus *Lagaropsylla*, which is widely distributed on molossids in the Afrotropical and Oriental regions, *L. mera* occurs on Northern Mastiff-bats in northern Australia and on *C. plicata* in Java. A number of other species of *Lagaropsylla* also is known from *C. plicata*. *Lagaropsylla incerta* has been recorded on *Mormopterus acetabulosus* on Madagascar and *Araeopsylla martialis* has been found on this bat on Réunion. All three species of *Coorilla*, which is endemic in Australia, are recorded from bats of the subgenus (*Micronomus*).

Molossids seem to be attractive to fleas. *Rhynchopsylla*, one of the two genera of non-ischnopsyllid fleas found on bats, is found on *Molossus*, *Eumops*, *Rhizomops* and some non-molossid bats in South America (Lewis 1972, 1974; Mardon & Allison 1978, 1982; Smit 1979; Lewis & Lewis 1985; Mardon 1986).

Another group of ectoparasitic insects known from molossids are polyctenid Hemiptera. One genus of about 16 species, *Hesperoctenes*, is from the Neotropical and Nearctic regions and the other, *Hypoctenes*, has five species found in the Afrotropical, Oriental and Australasian regions. There are no records of polyctenids from Australian molossids.

In the New World, polyctenids are found almost exclusively on molossids and there are fleas and cimicids on Neotropical members of the Molossidae and Vespertilionidae. These parasites are not found regularly on other Neotropical bats, suggesting a recent exploitation by these parasites from the Old World of



members of these two advanced and widespread bat families (Webb & Loomis 1977). A number of genera of cimicid bugs is recorded from molossids in all zoogeographical regions.

Twelve of the parasitic groups recorded from members of the Molossidae are acarids (ticks and mites) (Webb & Loomis 1977). Wenzel & Tipton (1966) recorded Dermanyssidae, Ixodoidea and Spinturnicidae from molossids. Ixodid ticks are not recorded as parasites of molossids in the New World (Webb & Loomis 1977). Roberts (1970) recorded larval *Argas* (*Carios*) from a bat identified as an Eastern Little Mastiff-bat and *Ixodes kopsteini* from *T. colonicus*.

Most raptors are diurnal and so do not normally come into contact with bats, although several species of raptors and crows have been recorded as attacking departing and returning dusk and dawn flights, respectively, of large cave colonies of molossids. A group of small falcons (length about 300 mm, wingspan about 800 mm), collectively called hobbies, are represented throughout the warmer parts of the world. They are swift flying, can be crepuscular and often hunt over water (Weick 1980). Czechura (1981) recorded the Australian representative of these falcons, the Australian Hobby (*Falco longipennis*) preying on bats, probably molossids, in open country. Owls also take some bats.

Molossids driven from their roosting sites in daylight are preyed upon by raptors and other birds such as kookaburras, magpies and butcher birds. Mumford (1980) recorded Black Kites (*Milvus migrans*) taking Little Mastiff-bats disturbed from their roost. Nothing is known of any mammalian or reptilian predation on molossids in Australia.

### Behaviour

The bifid lower incisors of most species are tucked below the cingulum of the lower canines and so are probably not used in food capture and manipulation. They could be used for grooming, like the pectinate incisors of some other mammals. The naked (furless) species of *Cheiromeles* have conical, rather than comb-like, incisors.

Temperate and tropical molossids have different temperature regulation mechanisms. Temperate species can spontaneously arouse from temperatures as low as 10°C, but tropical species succumb at 20°C (Lyman 1970).

Molossids are well known for roosting under metal roofs where temperatures may reach 40°C (Lyman 1970). High temperatures in pregnant females may speed up embryo development and shorten gestation period. Young bats will move away from heat if temperatures become intolerable (Barbour & Davis 1969).

The temperature regulation behaviours employed by molossids are patterns B1 (wide-range homeothermy), B2 (homeothermy attempted, partial torpidity at intermediate temperatures), C1 (narrow-range homeothermy in species which at other times enter complete torpor) and C2 (deep hibernation with complete torpor) (see Henshaw 1970 and literature cited). Minimal metabolic rates for Brazilian Free-tailed Bats of 1.63–2.0 ml O<sub>2</sub> g/hr (or 82–99% of the theoretical rate) are reported (see in Henshaw 1970 and literature cited).

To overcome the seasonal shortage of insect food brought on by cold conditions one of three behaviours can be employed:

1. migration to warmer areas where insects are still available;
2. reduction in activity, hunting only when insects are available and conserving energy by going into torpor;

- pass the adverse period in deep hibernation.

The first two behaviours are employed by different temperate species of molossid. No molossid is known to undergo deep hibernation. The foregoing behaviours involve accumulation of fat reserves, either for the migratory flight or to survive the reduced food intake during torpor or hibernation.

**Table 43.2** Dental formulae of selected molossid genera..

	LOWER INCISORS	UPPER PREMOLARS
<i>Mormopterus</i> (Malagasy)	3-3	1-1
<i>Mormopterus</i> (Neotropical)	2-2	1-1
<i>Mormopterus</i> (Australian) (= <i>Micronomus</i> )	2-2	2-2
Platymops	2-2	2-2
Sauromys	2-2	2-2

## BIOGEOGRAPHY AND PHYLOGENY

### Distribution

The Molossidae is a widespread family of bats found in the warmer parts of the world, occurring in all zoogeographic regions except Antarctica. The Molossidae is one of the three bat families found in both Old and New Worlds; the other two are the Emballonuridae and Vespertilionidae. These families show different levels of taxonomic similarity in the two hemispheres, suggesting different histories. In emballonurids, the genera found in the Old and New Worlds are very distinct, suggesting a long separation. In the Molossidae, there is a greater similarity; *Mormopterus* is common to both Old and New Worlds and may represent a relict distribution. The genus *Tadarida* was formerly considered to have a cosmopolitan distribution, but the New World forms have now been separated as discrete genera: *Nyctinomops* and *Rhizomops*.

In Australia, molossids are recorded from all States and Territories except Tasmania. For further details, see Strahan (1983) and Koopman (1984b).

### Affinities with other Groups

Within the Infraorder Yangochiroptera, distinguished from the other microchiropteran infraorder by the fusion of the premaxillary bones to the maxillaries, the Molossidae is placed in Superfamily Vespertilionoidea (Koopman 1984b). Their closest affinities, therefore, lie with the Vespertilionidae.

### Affinities within the Molossidae

Recent classifications of the Molossidae are those of Freeman (1981b), based on multivariate analysis which sorts the family at genus and species levels, and those of Legendre (1983), based on dental features which divide the Molossidae into three subfamilies and does not deal with categories below genus/subgenus.

The most recent critical listings of molossid species (Honacki *et al.* 1982; Hill 1986) treat taxa differently at the genus/subgenus level. Hill (1986) listed 13 genera, five subgenera and 91 species with 13 'forms that have recently been considered separate species but are here in the other earlier-named species'. Honacki *et al.* (1982) listed 87 species in 12 genera. These numbers differ because of descriptions of new genera as well as different views on taxa. I prefer to recognise as genera any subgenera which are consistently distinct, even in

minor details, and give much weight to distributional considerations. The subfamily Cheiromelinae is a very distinct grouping. Specialisations in the latter include a reduced tooththrow. From their varied diploid numbers, the genera in the Molossinae are not such a compact assemblage as those in Tadaridinae. Shortening of the tooththrow, which appears to be an apomorphy, is shown by *Molossus*.

The subfamily Tadaridinae has a diploid number of 48 throughout the included genera. Whilst Freeman (1981b) retained *Cynomops* and *Neoplatymops* as subgenera of *Molossops*, *Tadarida* was split into separate genera for *Chaerephon*, *Mops* and *Nyctinomops*. Full generic status was accorded *Mormopterus* (which has been considered at times as a subgenus of *Tadarida*). Legendre (1983) regarded *Chaerephon* and *Mops* as subgenera of *Tadarida*, but did not recognise *Xiphonycteris*, originally proposed as a genus, but at that time merged with *Mops* (Koopman 1975) and finally resurrected as a subgenus of *Tadarida* in its own right (El-Rayah 1981). Even with *Nyctinomops* and *Rhizomops* separated, the remaining species in *Tadarida* still form a more heterogeneous grouping than *Chaerephon* or *Mops*. *Tadarida* is more widespread geographically and members differ in number of lower incisors and structure of bacula. Because African species are the subject in the analysis of *Tadarida*, Koopman (1975) did not mention *T. australis*. This species would seem to fit in his *T. teniotis* group, but has a distinctive trifold baculum, very different from that of *T. teniotis*. The genus *Austronomus*, erected by Troughton (1941) for *T. australis*, may be justified.

The trend in *Tadarida sensu latissimo* towards a shortening of the jaw and tooththrow, including reduction of M3 to give a jaw with a stronger bite through increased leverage, follows the series *Tadarida sensu stricto* → *Chaerephon* → *Mops*, though some *Tadarida sensu stricto* have a powerful bite by virtue of their large size. This trend is correlated with diet; more powerful jaws are associated with a diet of beetles, while a diet of moths is associated with weaker or less powerful jaws.

The Australian species *Chaerephon jobensis* is very similar to the widespread Oriental and Wallacean *C. plicata*. The baculum of *C. plicata* is illustrated in Agrawal & Sinha (1973) under the name *T. plicata*, but no baculum has been found in any of the *C. jobensis* examined in Australia (F.R. Allison unpublished observation)

Hill (1986) gave *Platymops* and *Sauromys* generic status, Freeman (1981b) and Legendre (1983) regarded them as subgenera of *Mormopterus* and Honacki *et al.* (1982) included them in *Mormopterus*. Legendre (1983) also revived the name *Micronomus* Troughton (1944) as a subgenus of *Mormopterus*.

The *Mormopterus* species of Troughton (1944) from the three zoogeographical areas (see below) differ in dental formulae:

The subgenera of *Mormopterus* could well be elevated to generic status. There are even arguments for dividing the species in *Micronomus* further, based on such characters as skull profile and ratio of skull length:forearm length. Peterson (1985) reviewed the molossid bats allied with *Mormopterus* using phenetic analysis. *Sauromys* and *Platymops* were treated as genera and given separate phenograms for the sexes of the different taxa in *Mormopterus*.

### Fossil Record

The fossil record of the Molossidae to 1978 was summarised by Hand (1984b) and updated by Legendre (1985). There are no Australian records listed in the former account, but a footnote in the latter notes that Tertiary molossids have now been found in Australia (and Thailand). The fossil molossid from Australia does not appear to be ancestral to any genera currently in Australia (Hand 1987).

The Molossidae originated in Europe or North America. Legendre (1983) suggested the following scenario for the zoogeography of the Molossidae, using his concept of the classification at the genus/subgenus level. *Rhizomops* represents an ancestral genus of the Tadaridinae and the genera *Mormopterus*, *Nyctinomops*, *Otomops* and *Tadarida* differentiated from this stock. The genera *Mormopterus* and *Tadarida* radiated at the subgeneric level, the former with *Micronomus*, *Platymops* and *Sauromys*, the latter *Chaerephon* and *Mops*.

In the first instance, the invasion of the New World would have been by *Mormopterus* and then by *Rhizomops* and the Molossinae, restricting *Mormopterus* to refuge zones. *Mormopterus* had its distribution restricted in Africa and Asia by the radiation of the Tadaridinae. *Micronomus* would have had an endemic evolution in Australia. *Tadarida sensu stricto*, *Chaerephon* and *Mops* would have invaded Asia in successive waves, with *Mops* not reaching Australia.

## COLLECTION AND PRESERVATION

### Collection

Molossid bats may be picked up in roosts, when they are usually torpid or sluggish, either by hand or by using small hand nets. They may be trapped using mist-nets, bat-traps or other means as they emerge from their roost in an evening or may be smoked out of hollow trees or rock fissures. Though usually flying too high, they can be mist-netted or trapped over water when they come down to feed or drink. Trip wires set over water are often effective. Destructive collecting involves shooting with fine shot with a 12 or 20 gauge shot gun (.410 is usually too light), using a spotlight over water or on a flyway. Permits may be required to collect bats or even to handle them.

### Preservation

Specimens may be preserved as dry study skins or in preservative, usually ethyl alcohol. Treatment of freshly collected specimens with chloroform or ethyl acetate fumes will kill ectoparasites (and the bat) so they can be collected. Ectoparasites may be picked off live bats using a spirit or ethyl acetate moistened fine paint brush or cotton bud. If it is intended to collect parasites later, the bat must be kept frozen or in alcohol until this is done. Formalin is not suitable for ectoparasites, since clearing for microscopical examination is then difficult. Formalin or other preservative solutions may be needed for anatomical specimens or endoparasites after ectoparasites have been removed.

The skull may be extracted from spirit specimens through the tissue surrounding the mouth. The skull is removed when making a skin and the carcass may be saved for study and examination for endoparasites.

The concept of card skins for bats, pioneered by the British Museum (Natural History), does not seem to have gained general acceptance and liquid preservation is now the preferred technique.

Molossids are very prone to post-mortem fur colour changes and bleaching of pigmented skin in spirit. The preparation of bat study skins is described in a number of publications, including Villa-R. (1966) and Barbour & Davis (1969). Many biochemical and electrophoretic techniques often require that freshly killed specimens be frozen in liquid nitrogen for transport or storage.



### Laboratory Care

The maintenance of bats in captivity is detailed in Greenhall (1976) and Rasweiler (1977). Kingdon (1974) reported that ‘captive *Tadarida* are very hardy and not difficult to keep once the problem of feeding them is solved’. Hall (1982a) recorded keeping an individual of Beccari’s Mastiff-bat in captivity for 2 months.

## CLASSIFICATION

Family (or other Lower Taxon) Descriptions

Legendre (1983) divided the Molossidae into three subfamilies, only one of which is represented in Australia.

Tadaridinae Legendre 1983

Diagnosis: Straight tall upper incisors, separate and usually separate from canines. Lower incisors bilobed. Upper molars with a well-developed hypocone (with the exception of *Otomops*). Lower molars generally nyctalodont, occasionally mytodont in *Mormopterus*.

Type genus: *Tadarida* Rafinesque 1814

Genus and karyotype (diploid and fundamental numbers)

*Tadarida* 48, 54?

*Chaerephon* 48, 54? and 58

*Mormopterus* 48, 56

Five species of Molossidae presently are recognised in Australia (Mahoney & Walton 1988):

The White-striped Mastiff-bat (*Tadarida australis*) is characterised by a forearm length of 57–63 mm, a condylo-basal length of 23–24 mm, the pinnae are not joined across the top of the head, the skull is dorso-ventrally flattened, a gular gland is present, M3 is not reduced and the baculum is trifold.

The Northern Mastiff-bat (*Chaerephon jobensis*) is characterised by a forearm length of 46–52 mm, a condylo-basal length of 18–20 mm, the pinnae are joined across the top of the head, the skull is sinuate in profile with a sagittal crest, there is no gular gland and M3 is slightly reduced.

The Eastern Little Mastiff-bat (*Mormopterus norfolkensis*) is characterised by a forearm length of 36–38 mm, a condylo-basal length of 15 mm, the skull is sinuate in profile, PM<sup>1</sup> is developed, M3 is not reduced and the baculum is small and sagittulate.

Beccari’s Mastiff-bat (*Mormopterus beccarii*) is characterised by a forearm length of 35–41 mm, a condylo-basal length of 16–18, the skull is dorso-ventrally flattened and PM<sup>1</sup> is vestigial.

The Little Mastiff-bat (*Mormopterus planiceps*) is quite clearly a complex (P.R. Baverstock personal communication) and at this time no clear or workable characterisation can be provided. Too, the diagnoses of all Australian species of the genus *Mormopterus* are tentative until a thorough clarification of species limits is provided.

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