



FAUNA *of* AUSTRALIA

38. EMBALLONURIDAE

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DEFINITION AND GENERAL DESCRIPTION

The Emballonuridae comprises small to moderately large microchiropteran bats with a forearm ranging in length from about 35–95 mm. Members of this family are recognised by the following characteristics: typical chiropteran teeth; incomplete premaxillae which are represented by nasal branches only and are never fused with each other or with the maxillae; well-developed postorbital process; auditory bullae that are usually emarginate on the inner edge; the palate terminates in the plane of the last molars or, if produced behind this plane, narrows abruptly; the humerus with the trochiter is well developed but not as large as the trochin and not articulating with the scapula; neither tubercle of the humerus rises above the head of the humerus; the epitrochlea is not especially developed but does have a distinct spinous process, especially in *Taphozous* and *Diclidurus*; the second finger lacks bony phalanges; the third finger has two bony phalanges, the first of these is reflexed above the wing when at rest; the tail perforates the interfemoral membrane and appears on its upper surface distinctly back from the edge; the muzzle is without special cutaneous outgrowths (Miller 1907; Koopman & Cockrum 1967).

HISTORY OF DISCOVERY

The history of the taxon Emballonuridae was unravelled by Miller (1907). The family was first recognised as a distinct group by Gervais in 1855. At that time it was considered as a tribe of Vespertilionidae under the name Emballonurina. Most of the genera included in the Emballonuridae by Miller (1907) are still recognised today. More recent genera and their treatment by major revisers are charted in Table 38.1.

Of more direct interest in Australia is the prevailing confusion concerning the status of *Taphozous* E. Geoffroy 1813 and *Saccolaimus* Temminck 1838. Dobson (1875) compounded this confusion by transferring species in this latter genus to *Taphonycteris*, which Miller (1907) synonymised with *Taphozous*. Thomas (1915, 1922) considered *Taphozous* and *Saccolaimus* as distinct and in his diagnosis emphasised differences in their auditory bullae. Troughton (1925) rediagnosed *Taphozous* and *Saccolaimus* and was the first to attribute the initial

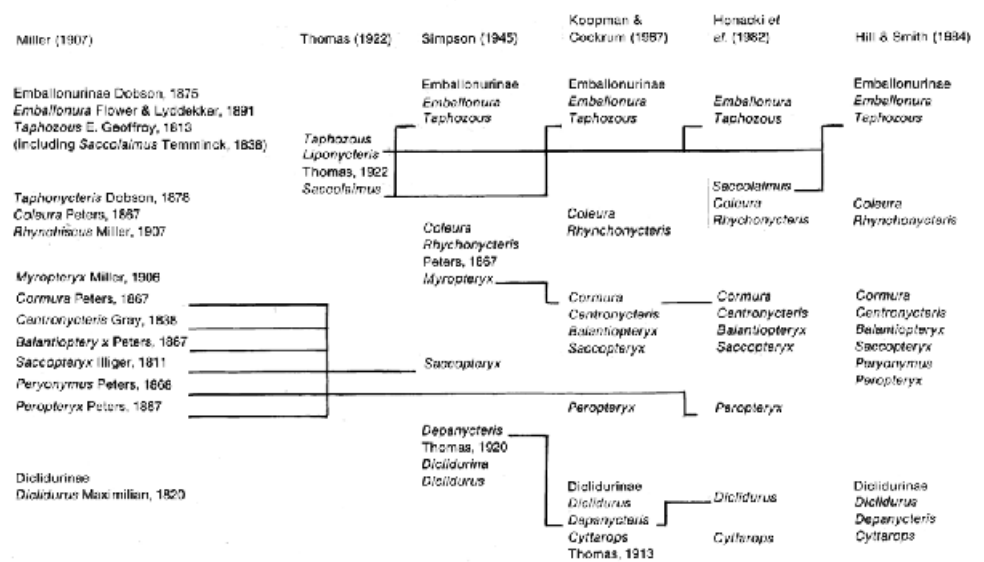


Table 38.1 A summary of past and present generic arrangements in the Emballonuridae.

usage of *Saccolaimus* to Temminck rather than to Lesson 1842. Tate (1941d) considered *Taphozous* and *Saccolaimus* as subgenera of *Taphozous*. Barghoorn (1977), in his redescription of the fossil emballonurid *Vespertiliavus* Schlosser 1882, again separated *Taphozous* and *Saccolaimus* on the basis of many features of the basicranium and ear region – a view supported by Koopman (1984a), but not by Hill & Smith (1984). Robbins (1983b), using electrophoretic and immunological data, considered *Taphozous* and *Saccolaimus* to be distinct.

Taphozous australis Gould 1854 and *Saccolaimus flaviventris* (Peters 1867) were the first species ascribed to their respective genera from Australia. In Australia there are 13 named forms of emballonurids. The species are: Common Sheathtail-bat (*Taphozous georgianus*) Thomas 1915 – including *T. troughtoni* Tate 1952; North-eastern Sheathtail-bat (*T. australis*) Gould 1854 – including *T. fumosus* de Vis 1905; Hill's Sheathtail-bat (*T. hilli*) Kitchener 1980; White-striped Sheathtail-bat (*T. kapalgensis*) McKean & Friend 1979; Yellow-bellied Sheathtail-bat (*Saccolaimus flaviventris*) Peters 1867 – including *S. hargravei* Ramsay 1876 and *S. affinis insignis* Leche 1884; Papuan Sheathtail-bat (*S. mixtus*) Troughton 1925; Naked-rump Sheathtail-bat (*S. saccolaimus*) Temminck 1838 – including *S. nudicluniatus* de Vis 1905 and *S. granti* Thomas 1911. The synonymy of *S. nudicluniatus* with *S. saccolaimus* follows Goodwin (1979), but this matter requires a more detailed study.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Emballonurids are amongst the most distinctly coloured of the Australian bats. Generally the pelage of emballonurids is brown or greyish brown, although some are blackish and *Diclidurus* is white or greyish white. Species of *Taphozous* and *Saccolaimus* frequently have white spots on the body and pale cream or whitish underparts. The Naked-rumped Sheathtail-bat is brownish with distinctive white dorsal flecks and has a naked or unfurred rump region; the Papuan Sheathtail-bat is dark brown above and pale buff-brown below; the Yellow-bellied Sheathtail-bat is glossy jet black on the back and white to yellow underneath and the White-striped Sheathtail-bat is pale brown with two broad white ventral stripes.

The Papuan Sheathtail-bat and *Taphozous* species have a well-developed radio-metacarpal pouch (Fig. 38.1). The hind limbs are slender (Fig. 38.2). The tail does not extend through the uropatagium, but emerges through the dorsal surface at about half way along the tail (Fig. 38.2). The muzzle is pointed, lacks foliaceous appendages and the tragus is simple and rounded (Fig. 38.3). A lateral view of the cranium and lower jaw are shown in Figure 38.4. The teeth are of the normal insectivorous type (Fig. 38.4) and vary from 30 to 34 between genera. The dental formula for the Australian species is I 1/2 C 1/1 PM 2/2 M 3/3.

Body Wall

The epidermis of bats, particularly tropical species such as *Taphozous* and *Saccolaimus*, is of considerable functional interest because of its expanse and the role it may play in water loss (Quay 1970a). Australian *Saccolaimus* and *Taphozous* roost in trees and or caves. When Common and Hill's Sheathtail-bats roost in deep caves, they usually prefer sites that receive twilight and do not seek out the more humid environment of the deeper parts of caves as do *Hipposideros* and *Macroderma*. Because increased humidity may reduce water loss this suggests that water conservation is not a major concern of Australian emballonurids.

Figure 38.1 Radio-metacarpal pouch on the ventral surface of the wing of the Common Sheathtail-bat, *Taphozous georgianus* (© ABRS)
[F. Knight]

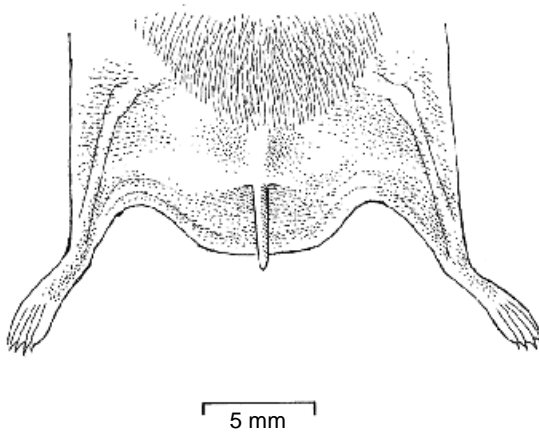
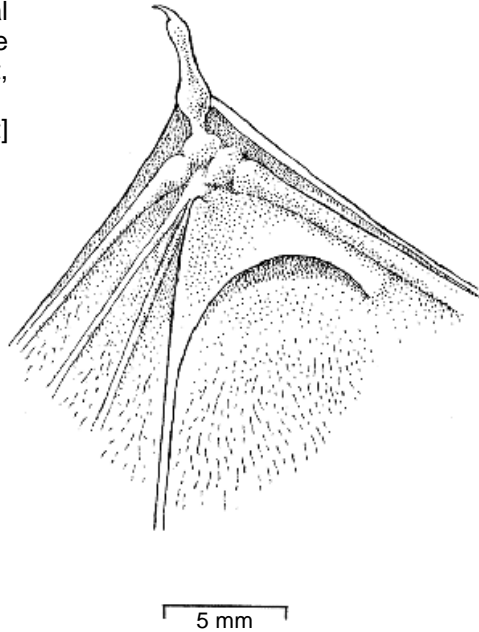


Figure 38.2 Dorsal view showing the relationship of tail and flight membrane in Emballonuridae. (© ABRS)
[F. Knight]

Enormous unilocular and yellowish fat deposits accumulate at the base of the tail and in the uropatagium in arid adapted *Taphozous kachensis* (= *nudiventris*) of India (Brosset 1962a). This accumulation is related to prolonged periods of quiescence in the dry season when this bat remains awake but does not fly. No similar fat deposits are known in Australian emballonurids although Common and Yellow-bellied Sheathtail-bats have extensive reserves of mesenteric and cutaneous fat throughout the body. In Yellow-bellied Sheathtail-bats at least, such fat deposits show no clear seasonal trend in abundance.

Skeletal System

The morphology of the scapula, pelvic girdle and particularly the humerus show considerable variation between the families of bats. Some of these aspects have been touched upon above. In emballonurids, the scapula is oval in outline. The coracoid border has a deep notch which has a ventrally directed flange. The coracoid process is untapered and a postglenoid pit is present in the axillary border (Walton & Walton 1970). The clavicle is large, quite long, curved and typically chiropteran. Only in the subfamily Diclidurinae does the clavicle deviate from this form by having an anterior process on each side that extends as a sheet of bone (Vaughan 1970d). Modifications to the humerus, which are widespread in chiropterans, are poorly developed in emballonurids. For

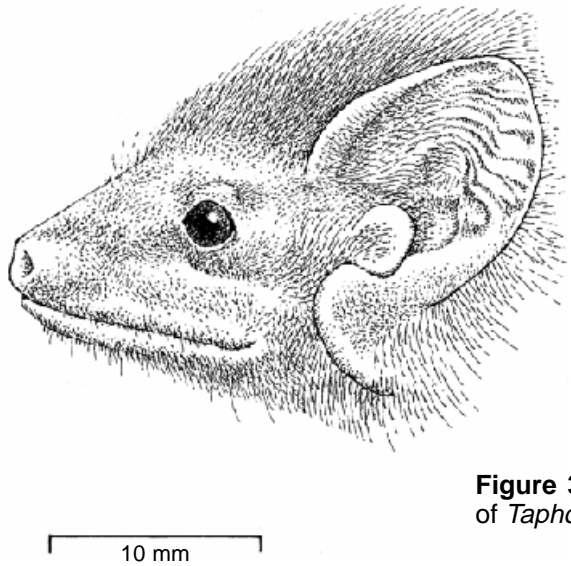


Figure 38.3 Lateral view of the head of *Taphozous saccolaimus*. (© ABRS) [F. Knight]

example, the greater tuberosity does not extend beyond the head (also a condition of the 'primitive' Pteropodidae), the medial ridge is weakly developed and the medial epicondyle has no spinous process (Vaughan 1970d). The shaft of the humerus is also curved and the distal articular surfaces are out of line with the shaft (Vaughan 1970d; Walton & Walton 1970). The humerus does not articulate with the scapula in emballonurids except in *Saccopteryx bilineata* where there is an insecure contact in certain positions (Vaughan 1970d). As befits their roosting habit, the pelvis of the emballonurids is moderately robust and shares pelvic characters with many other chiropteran families (Vaughan 1970d). There is no dorsal ischial tuberosity and the shape of the obturator foramen is variable. There are five sacral vertebrae (Walton & Walton 1970). The fibula is complete and thread like and the tibia flattened or grooved posteriorly in *Diclidurus* (Koopman & Cochrum 1967).

Little is published on the morphology of the soft tissues, organs or the physiology of emballonurids. Lyman (1970) suggested from the partial studies on the thermoregulation of *Taphozous kachensis* (= *nudiventris*) and *Taphozous melanopogon* in India, that members of this family have a circadian pattern to their body temperature with low temperatures occurring during the period when the animal is inactive. These two species are capable of rewarming from low temperatures by metabolic activity, but body temperatures below 12–16°C are lethal to *T. melanopogon*.

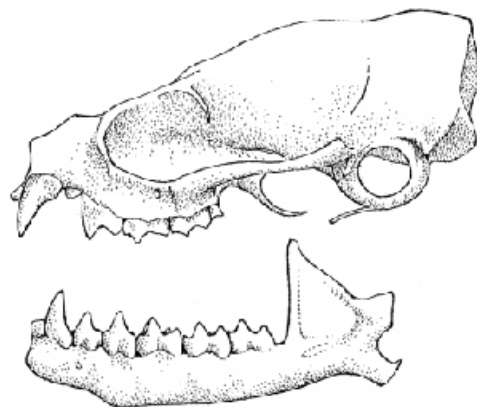


Figure 38.4 Lateral view of the cranium and mandible of *Taphozous georgianus*. (© ABRS) [F. Knight]

Endocrine and Exocrine Systems

Quay (1970a) recorded six types of integumentary glandular areas in emballonurids. These are: (i) propatagial glandular sac, especially in adult males; (ii) labial gland; (iii) chin gland; (iv) gular gland and pouch; (v) median chest gland and (vi) uropatagial glandular pouch. Males of some *Taphozous* species (Hill's, North-eastern and White-striped Sheathtail-bats) as well as males of *Saccolaimus* (Papuan, Yellow-bellied and Naked-rumped Sheathtail-bats) have pronounced throat pouches. These throat pouches are less developed in the females and are absent or rudimentary in females of the Yellow-bellied Sheathtail-bat (Hall & Gordon 1982) and the Australian Naked-rumped Sheathtail-bat (Compton & Johnson 1983). Their absence in the latter species contrasts with the observation of Dobson (1878) who recorded them as well developed in both male and female Naked-rumped Sheathtail-bat specimens from India, Ceylon, Singapore and Java.

It is probable that the throat pouches of the Old World emballonurids serve a function that is reserved to the propatagial pockets of the New World species in marking territories. For example, the Indian *Taphozous longimanus* exudes a red secretion which has a strong smell in the rut (Brosset 1962a). Also, a large sebaceous gland posterior to and opening into the non-glandular surface of the gular pouch is present in male Yellow-bellied Sheathtail-bats. Females of this species have no throat pouches, but they do have several sudoriferous glands that lead to the surface via short coiled ducts (Hall & Gordon 1982). The depth of the gular pouch in male Hill's Sheathtail-bats is correlated with their reproductive condition and the pouch may play some role in male social behaviour (Kitchener 1976b).

Reproduction

The reproductive patterns of emballonurids are poorly known (Carter 1970), although the few studies available indicate that members of this family are quite variable in this regard.

Kitchener (1973b, 1976b) reported that female Common and Hill's Sheathtail-bats (as *T. georgianus*) are apparently monoestrous. They give birth to a single young between October and February, although it is possible that Hill's Sheathtail-bat has a slightly extended season of births. Only the right ovary is functional. Reproductive organs of females show a reduction in activity from mid-autumn to the end of winter. Males are in active spermatogenesis throughout the year. The position of the testes varies seasonally: scrotal in summer and more abdominal in autumn, winter and spring. Hall (1983a) reported groups of breeding female North-eastern Sheathtail-bats in September and noted that most births probably occur in October or November. Testes are abdominal in September but scrotal in April. On the other hand, the Indian *Taphozous longimanus* has a very different pattern of reproduction (Gopalakrishna 1955). It is also monotocous, but is polyoestrous and gives birth to young throughout the year. Both ovaries are equally active and pregnancies alternate between the uterine horns.

Compton & Johnson (1983) found Naked-rumped Sheathtail-bat females in advanced stages of pregnancy or with attached young in mid-December. Hall & Gordon (1982) collected female Yellow-bellied Sheathtail-bats with advanced pregnancies in mid-November. Examination of extensive collections of Yellow-bellied Sheathtail-bats shows that pregnancy is almost always in the right uterine horn. A single young is born between December to approximately mid-April. Subadults are collected only in January and February. In males, the position and weight of the testes and size of the gular pouch do not show marked seasonal changes.

Embryology and Development

Rasweiler (1979) records that the Colombian emballonurid *Peropteryx kappleri* has tubular morulae of up to 33 cells and notes that this embryonic development proceeds somewhat further in the oviducts than is usual in chiropterans.

Our knowledge of the foetal membranes and placentation of emballonurids derives from studies on the Indian *Taphozous melanopogon* and *T. longimanus* (Gopalakrishna & Karim 1979). These species do not appear to have developed any unique features in this regard.

Amongst chiropterans, emballonurids are very large at birth relative to their adult size (Davis 1944). Although little is known of their postnatal development (Tuttle & Stevenson 1982), the attachment of young to female Common Sheath-tail-bats is thought to be brief (Kitchener 1973b). In the case of *Saccopteryx bilineata* and *S. leptura*, the young are large at birth and fly at 1–2 weeks of age but remain with their mothers during the day until they are several months old. Young of both these *Saccopteryx* species are not found at night on the diurnal roosts and young *S. bilineata* are known to be carried to other trees and hidden separately while their mothers forage (Bradbury & Emmons 1974).

NATURAL HISTORY

Life History

Our knowledge of the life history of emballonurids largely devolves on the comprehensive study by Bradbury & Emmons (1974) of three tree-roosting Trinidad species (*Saccopteryx bilineata*, *S. leptura* and *Rhynchonycteris naso*). These three species indicate that emballonurids show a range of social behaviour and variety of group structures, ranging from single male and female pairs to up to about 40 individuals. Depending on species, these large aggregations may have approximately equal numbers of both sexes or a single male with a 'harem' of females. The behavioural repertoire also differs widely between these species. Males of *S. bilineata* actively defend territories and perform elaborate vocal, visual and, presumably, olfactory displays. On the other hand, male *S. leptura* are not territorial and do not perform elaborate displays in competition for females. Young are born to the two *Saccopteryx* species over a period of 13–28 days. Despite this strict seasonality of births the social structure is constant throughout the year.

Behaviour

The large *Saccolaimus peli* of the African rainforests is solitary and forms pairs only at breeding times (Rosevear 1965). Almost nothing is published on the social behaviour of Australian emballonurids. This is most unfortunate considering the potential shown by members of this family for involved social behaviour.

Two species of Australian *Saccolaimus* (Yellow-bellied and Naked-rumped Sheath-tail-bats) roost in hollows in trees. This is characteristic of bats which have pelage markings and stripes (Kunz 1983) and it is likely that the other Australian *Saccolaimus* species roost in trees or amongst vegetation. The Yellow-bellied Sheath-tail-bat tends to be solitary when roosting, but does form small groups of two to six individuals, particularly in late winter and spring (Hall & Richards 1979). Compton & Johnson (1983) observed a colony of Naked-rumped Sheath-tail-bats roosting in hollows in poplar gums near Townsville, Queensland, but did not comment on their numbers or group structure.

Unlike the Indian emballonurids *Taphozous melanopogon* and *T. perforatus*, which roost almost exclusively in man-made structures (Brosset 1962a, 1962b), Australian *Taphozous* species usually roost in caves and cracks, although they will readily inhabit mine shafts and adits. These Australian species are solitary or occur in groups of usually less than 20 individuals. Groups of Hill's and Common Sheathtail-bats usually contain approximately equal numbers of both sexes (Kitchener 1976b, 1978).

Ecology

The Common Sheathtail-bat feeds continuously on insects, particularly beetles (Vestjens & Hall 1977), while flying above the vegetation canopy and detects insects at distances of at least 2 m (Fenton 1982b; McKenzie & Rolfe 1986). Other Australian emballonurids also appear to feed continuously above the canopy on insects (McKean 1983; Richards 1983a, 1983b; McKenzie & Rolfe 1986), although in mallee or open country Yellow-bellied Sheathtail-bats feed closer to the ground (Richards 1983b). While feeding, these species make a series of noises that are clearly audible to humans.

The Yellow-bellied Sheathtail-bat may be migratory in southern Australia as there are several reports of exhausted individuals of this species in open situations (Richards 1983b). The possibility of it migrating through South Australia in autumn was canvassed by Aitken (1975) who noted that the few specimens from that State (all from the south-east) were collected between late March and the end of May. Populations of Common Sheathtail-bats appear to be at least locally mobile in the Pilbara and Murchison regions of Western Australia. Daytime flights are not reported for undisturbed Australian emballonurids, although such flights for the purpose of feeding beneath the tree canopy are reported for the external roosting *Saccopteryx bilineata* (Bradbury & Emmons 1974).

Economic Significance

Although bats are known to be vectors for a number of diseases of man, the literature summarised by Constantine (1982) suggested that in this regard emballonurids are relatively little threat to man. Constantine (1982) reported that the guano of several species of emballonurids in Trinidad, Colombia and East Africa have faeces that harbour pathogenic fungi (*Histoplasma*, *Scopulariopsis* and *Microsporum*) that have airborne spores which could cause serious and even fatal lung infections in man. *Peropteryx macrotis* in Colombia carries *Trypanosoma cruzi*, a protozoan which produces Chagas' Disease in man. *Diclidurus virgo* in Trinidad carries rabies.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Emballonuridae, which comprises 12 to 13 genera and 51 species (Honacki, Kinman & Koepl 1982; Hill & Smith 1984) occurs in both Hemispheres (Fig. 38.5), but is confined mainly to the tropics. The subfamily to which the Australian genera belong (Emballonurinae) occurs in both the Old and New Worlds. Members of the other subfamily (Diclidurinae) are confined to the American tropics (Koopman 1970). Within Australia, three species (Hill's, Common and Yellow-bellied Sheathtail-bats) are found outside the subtropics – the Western Australian *Taphozous* species to approximately 27°S (Kitchener 1983a, 1983b) and Yellow-bellied Sheathtail-bats in Victoria to about 38°S (Richards 1983b).

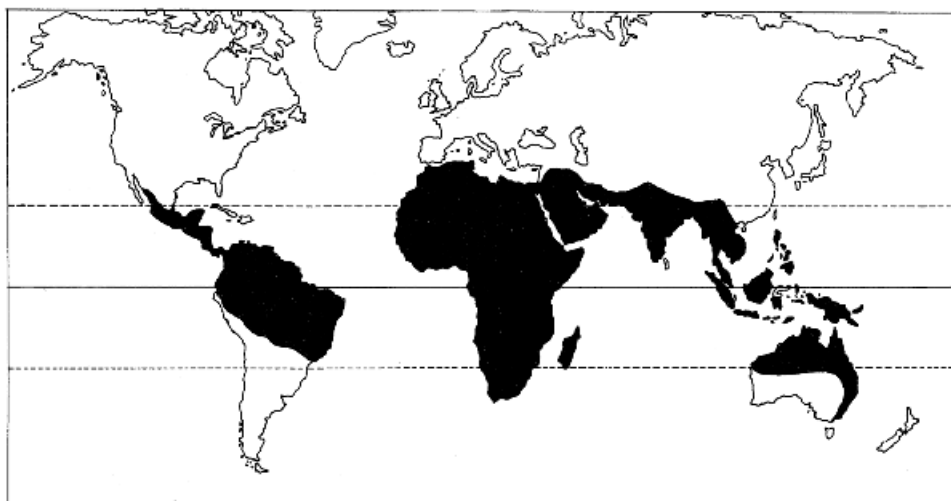


Figure 38.5 Distribution of Emballonuridae. (Modified from Koopman 1970)

The concentration in the tropics of emballonurids, and bats in general, is probably related to the greater diversity and availability of food in all seasons (Findley 1976). Both Hill's and Common Sheathtail-bats readily inhabit vacated mine shafts and adits and in some localities are present only in such situations. This suggests that availability of roost sites, rather than food, may be influential in determining the local distributions of these species. This is in accord with Tamsitt (1967) who considered roost sites an important determinant of the local distribution of bats.

The distribution of species of *Saccolaimus* in Australia would appear to be influenced, in part, by availability of suitable trees for roosts. In the case of the Naked-rumped Sheathtail-bat, the poplar gum, *Eucalyptus alba*, may be important (Compton & Johnson 1983).

Affinities with Other Groups

The phylogenetic relationships of the Emballonuridae have been the focus of considerable debate for many years. In the last century, members of the family have been variously related by their classification to representatives of the following modern families: Vespertilionidae, Furipteridae, Mystacinidae, Noctilionidae, Mormoopidae, Molossidae and Rhinopomatidae.

Miller (1907) considered the emballonurids next to the rhinopomatids in combining the greatest number of primitive characters with the least degree of specialisation. He placed members of these two families, along with those in the Noctilionidae, as among the more primitive of the Microchiroptera. Simpson (1945) also recognised the close relationship between the Emballonuridae, Rhinopomatidae and Noctilionidae together in the superfamily Emballonuroidea. Walton & Walton (1968) suggested that the Emballonuridae, Phyllostomidae and Noctilionidae are monophyletic; they gave little credence to the suggestion of Dobson (1875) that the Noctilionidae forms a connecting link between the Phyllostomidae and the Emballonuridae. More recently, Hill (1974) allied his new family, Craseonycteridae, to the Emballonuridae and Rhinopomatidae.

Affinities within the Emballonuridae

Smith (1976) applied a cladistic analysis to review the relationships of the emballonurids. He noted that an emballonuroid ancestry generally has been accepted as the base for the evolution of the Microchiroptera, but considered that this view is based more on the antiquity of the group than on their characteristics. He pointed out that emballonurids show a reduction in size and number of premolars, rostral inflation, unfused and unique form of the premaxillaries, a trend towards complicated osseous processes on and posterior to the dorso-nasal plate, complicated basisphenoid pits and specialisation of the humerus. These characters suggest a more specialised state than would be expected of an ancestral group. This led Smith (1976) to suggest that the several lineages of Microchiroptera probably radiated from a widespread palaeochiropteran grade and that the Emballonuridae form a monophyletic group with the Rhinopomatidae and Craseonycteridae. Robbins (1983b) examined the evolutionary relationships of 12 genera and 17 species of emballonurids using electrophoretic data and immunological distance values from the microcomplement fixation method. These data indicate three major subdivisions within the family. The eight genera from the New World form one monophyletic group. The Old World genera are separable into two groups: *Saccolaimus* and *Taphozous* in one and *Emballonura* and *Coleura* in the other. There is an unresolved trichotomy of the three lineages using electrophoretic data, although the immunological data show that the *Emballonura-Coleura* clade is related more closely to the New World clade than to the other Old World genera. The evolutionary distinctiveness of the subfamily Diclidurinae is not substantiated.

Fossil Record

Despite its fragmentary fossil record, the Emballonuridae appears to have originated in the Old World and spread later into both the New and Old World tropics (Legendre 1980). The majority of Tertiary fossil emballonurids are from late Eocene and Oligocene sediments in Europe and are referable to the extinct genus *Vespertiliavus* (Schlosser 1887) which is closely related to living *Taphozous* and *Saccolaimus* species (Barghoorn 1977). The only other Neogene emballonurid from Europe is a species similar to *Taphozous* from Port-La-Nouvelle in Ande, France (Legendre 1980). Emballonurids first appeared in Africa in the early Miocene and two species are recognised from a few bone fragments from a deposit in Kenya. One is an indeterminate emballonurid (Butler 1969) and the other was named *Taphozous incognita* by Butler & Hoopwood (1957). There are no known pre-Pleistocene emballonurid fossils from the New World.

Although *Vespertiliavus* is the oldest known emballonurid, Barghoorn (1977) did not regard it as ancestral to the family as a whole. Because *Vespertiliavus* does not appear to have given rise to European and African fossil species of *Taphozous*, Legendre (1980) postulated at least two phases of emballonurid migration between Africa and/or Asia and Europe. The first phase, in the Late Eocene, involved species of *Vespertiliavus*. The second phase, in the Middle Miocene, involved *Taphozous* species. It is likely that emballonurids spread into tropical regions of the Old World during the Oligocene before the middle latitudinal climatic deterioration of the Late Miocene. In the Neotropics, they underwent considerable diversification such that nine genera and 18 species are recorded from the Neotropics (Koopman 1970).

It is probable that emballonurids reached Australia via the Orient during the Middle Miocene. Since about 15 mybp, when the Sula Peninsula extension of Australia/New Guinea collided with east Sulawesi, there has been a chain of islands from Sulawesi through Banggai, Sula, Ceram and New Guinea to

Australia through which emballonurids could island hop. An alternate route to Australia is along the Lesser Sunda islands to the east of Java; these islands have been formed since the Late Miocene. Emballonurids appear to readily disperse over water barriers. Species of both *Emballonura* and *Taphozous* are common on the Indonesian islands and *Emballonura monticola* has established on Krakatau since the sterilisation of this island by a volcanic eruption in 1883.

The Common Sheathtail-bat, along with Dusky Horseshoe Bats, *Hipposideros ater*, and Ghost Bats, *Macroderma gigas*, is found in caves in parts of northern Australia (Kitchener 1978) and the North-eastern Sheathtail-bat shares caves with Eastern Horseshoe Bats, *Rhinolophus megaphyllus*, in north-eastern Queensland (Hall 1983a). The absence of *Taphozous* from the Middle Miocene deposits at Riversleigh, north-western Queensland, which contain representatives of *Macroderma* and *Hipposideros*, may indicate that emballonurids had not reached Australia before the availability of the island routes referred to above.

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