



FAUNA *of* AUSTRALIA

47. MURIDAE

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Lakeland Downs Mouse—*Legadina forresti* [D. Moro/CALM]



Greater Stick-nest Rat—*Leporillus conditor* [F. Knight/ANPWS]



Northern Hopping Mouse—*Notomys aquilo* [F. Knight/ANPWS]



House Mouse—*Mus musculus* [D. Moro/CALM]



False Water-rat—*Xeromys myoides* [F. Knight/ANPWS]



Water-rat—*Hydromys chrysogaster* [J. Wombey]



Carpentarian Rock-rat—*Zyzomys palatalis* [C.R. Trainor/PWCNT]



Sandy Inland Mouse—*Pseudomys hermannsburgensis* [J. Wombey]



New Holland Mouse—*Pseudomys novaehollandiae* [CSIRO Wildlife & Ecology]



Hastings River Mouse—*Pseudomys oralis* [E. Slater/NSW NPWS]

DEFINITION AND GENERAL DESCRIPTION

The classification system of Carleton & Musser (1984) which deals with the Suborder Myomorpha and the Superfamily Muroidea is followed in this chapter. However, in contrast to these authors, below the level of superfamily the term Muridae is used in the restricted sense of Simpson (1945) and Honacki, Kinman & Koeppl (1982) and does not include the cricetids (for example, hamsters, voles and lemmings) or rhizomyids (bamboo and African mole-rats). Other authors treat them as a subfamily (Murinae) of the Family Cricetidae (Carleton & Musser 1984). In the current state of knowledge of the higher taxonomy of these rodents, either course seems acceptable. We made our choice on the quite pragmatic and parochial basis that it facilitates discussion on the groupings within Australian rodents. The Muridae is best defined by complex details of the molar cusps (see Carleton & Musser 1984: under Murinae).

The Family Muridae is one of the largest groups of rodents with some 460 recent species grouped in 117 genera. They are often the most numerous mammal over much of their range. They are distributed over the whole of the Old World, and the highest number of species is found in the Indo-Australian Region, where the family is believed to have arisen.

Australian murids display the typical conservative form of other 'Old World Rats and Mice'. Along with other members of the family, they all have five digits on both fore- and hind feet and the thumb (pollex) is rudimentary. The dental formula is typically murid except for *Hydromys* and *Xeromys*, in which only two upper and two lower molars are present. Murid molars have roots. As in all other rodents, the incisors are chisel-shaped with an anterior edge of enamel with the bulk of the tooth made of dentine. In life habits, Australian murids are mostly terrestrial and quadrupedal although some are aquatic, some arboreal and species of one genus (*Notomys*) are saltatorial (hopping) and bipedal. There are no gliding forms. To our knowledge there are no characteristics which separate Australian murids, as a whole, from their counterparts in other parts of the world.

HISTORY OF DISCOVERY

There are 59 recognised modern species of native murid (those known to have been extant since Europeans first settled the continent). The history of their discovery can be divided into several periods (Fig. 47.1).

The first species to be described was the Water Rat (*Hydromys chrysogaster* Geoffroy 1804), but between then and 1830 only one other species was described. The first major period of discovery was between 1830 and 1860 when 18 new species (as recognised today) were named (Fig. 47.1). During this time, the partnership of Gould (taxonomist) and Gilbert (collector) was very active. Gould named many species of Australian murid, 10 of which are considered valid today. Most of the specimens came from the settled areas of the colonies and a few resulted from collecting in the tropical north. The majority of the early material went to British and European museums where the type specimens are now held. Many names that were proposed during this period have fallen to synonymy. Descriptions were often based on morphological characters which show intraspecific variation (for example, fur colour, tail colour, body and cranial size).

The next major period of discovery occurred between 1880 and 1940, with a gap during World War I. Many collectors were involved, notably Shortridge in Western Australia, Dahl in the far north, members of the Horn Expedition in central Australia, and Bolam along the transcontinental railway. Many of the

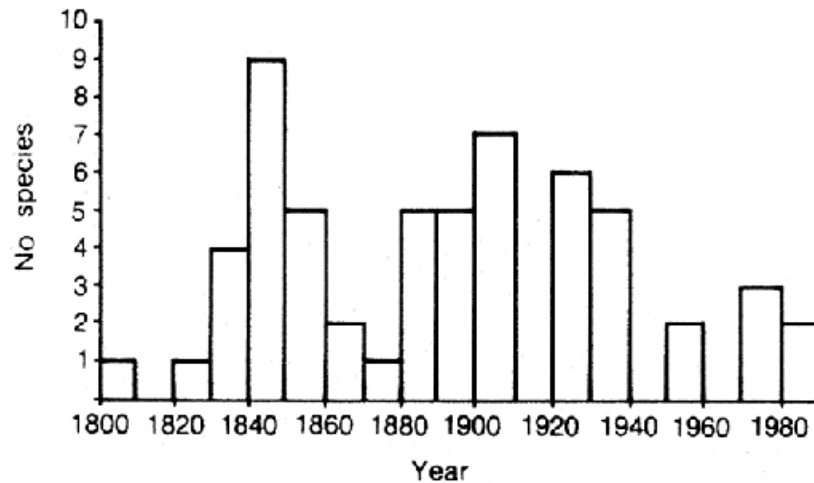


Figure 47.1 Periods of description of new species of Australian Muridae. Only species recognised today included.

species described during this period were from remote areas such as the arid interior and tropical north. Some were rare species inhabiting the areas surveyed during the first period of discovery. Oldfield Thomas recognised 15 species and was the major murid taxonomic contributor of this era.

Since 1940, only seven new species have been recognised. With the exception of two described by Tate (1951a), their existence has been demonstrated by the new taxonomic techniques of electrophoresis, karyotype comparison, sperm morphology and morphometric analysis. More species will probably be described in the near future, particularly in the genus *Pseudomys*. Extensive field collections have been conducted, obtaining live specimens of most species of Australian rodent (Robinson *et al.* 1978). These collections formed the basis of an extensive rethinking of the phylogeny of the family in Australia.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Most Australian murids resemble the laboratory rat and mouse. Limbs and hind feet are short or of only moderate length, the length of the tail may be shorter or longer than the head and body, and the ears are broad and rarely elongate. Tate (1951a) provides a good description of many external characteristics including the pelage, moult pattern, eye, ear, lip, manus and pes.

Certain groups diverge from the general body form. Tree rats of the genera *Mesembriomys* and *Conilurus* have a long tail with a bushy tip and have broad hind feet. The ears are long in *Conilurus*, hence the name Rabbit-rat. In some arboreal/scansorial genera the tail is entirely prehensile (*Pogonomys*) or partially so (*Melomys*). The hopping mice (*Notomys*) have an elongated hind limb and foot, and the tail, which is longer than the head and body, has a brushy tip. The Water Rat and False Water Rat (*Xeromys myoides*) have dense water-repellent fur and a flattened head with small, dorsally placed eyes. Water Rats have partially webbed hind feet. Rock-rats (*Zyzomys*) have a fattened tail. The number of mammae (teats) varies among genera and, within *Rattus*, among and within species. All non-*Rattus* genera have four mammae, except *Pogonomys* species which have six, and species of *Rattus* have up to 12.

Skeletal System

No studies have been published on the postcranial skeleton of Australian Muridae except with reference to fossil deposits. Few major divergences from the typical murid plan should be expected. In *Notomys*, bipedal locomotion may have resulted in some specialisations of the skeleton such as forelimb reduction (Marlow 1969).

The skulls of Australian Muridae do not differ markedly from their relatives outside the region (Tate 1951a; Carleton & Musser 1984). All Australian species have cuspidate molars and three pairs of molars in both upper and lower jaws with the exception of water rats which have two pairs. Herbivorous species have relatively broader teeth than omnivorous/granivorous species.

Tate (1951a) recognised that several of the Conilurini (see classification) have some cranial features in common: the post-squamosal sinus is well developed; the coronoid process of the mandible is reduced; the incisive foramina extend well into the premaxillae (the *Melomys/Uromys* group also shares this feature); and the first upper molar has three roots as opposed to five in *Rattus* and four or five in *Melomys/Uromys* (Fig. 47.2). Species with very large eyes, such as those of *Notomys* and *Conilurus*, have a large optic foramen. The tympanic bullae tend to be more inflated in species which live in open habitats such as the arid interior.

Locomotion

Australian murids seem to be confined mostly to quadrupedal, terrestrial locomotion although little work has been done to document this. Studies of foot tracks (Morrison 1981; Triggs 1984) have helped show that the small quadrupedal species have a walking and hopping gait. The tail is dragged along the ground in some large species (the Water Rat and some *Rattus* species).

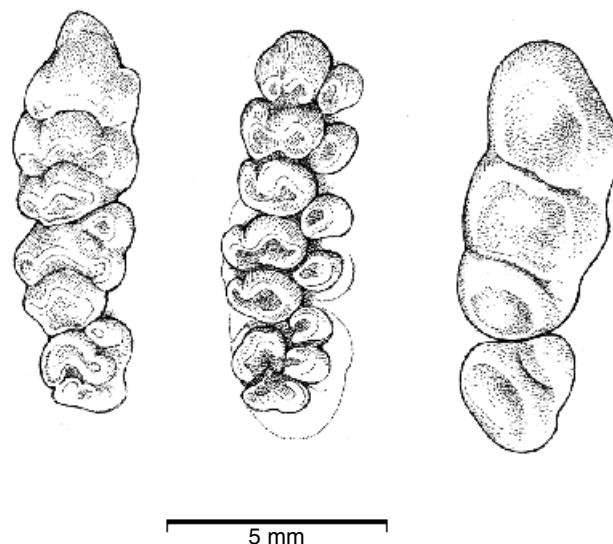


Figure 47.2 Upper molar tooth rows of, from left to right, Long-haired Rat (*Rattus villosissimus* Murini) with lingual and labial cusps of approximately the same size; Greater Stick-nest Rat (*Leporillus conditor* Conilurini) with labial row of cusps reduced; Water Rat (*Hydromys chrysogaster* Hydromyini) with molar row reduced to two teeth with a more simple cusp pattern.

[F. Knight]

Notomys species are bipedal at high speeds and quadrupedal at low speeds (Marlow 1969; Baudinette, Nagle & Scott 1976b). Bipedally, the maximum stride length of the Fawn Hopping-mouse (*N. cervinus*) is 689 mm with a mean speed of 2.9 m/sec. Stride length drops to a mean of 212 mm when travelling quadrupedally. Stride frequency of the Spinifex Hopping-mouse (*N. alexis*) levels off at about 390 strides/min. When running bipedally, the tail is held highest when landing, presumably for balance. *Conilurus* species also have been observed to bound with the tail held high. Based on structural features of the skull, Tate (1951a) suggests that the members of this genus could be leapers.

The energetic cost of bipedalism in small mammals has been the subject of some debate. Early studies concluded that there was a large saving when Notomys travelled at high speeds (Baudinette *et al.* 1976b; Dawson 1976). However, Thompson *et al.* (1980) found that bipedalism was not cheaper energetically than quadrupedalism and speculated that the benefits of bipedal locomotion must be related to predator avoidance in open environments.

All Australian murids probably have the ability to swim, some better than others. The Water Rat (and probably the False Water Rat) spend a good deal of time in the water. The thick tail aids propulsion when diving and swimming below the surface. The limbs are placed more laterally than in other species. Water Rats are said to have a clumsy gait on land, taking 'low hops with the body leaning well over' (Troughton 1941).

No Australian murid is strictly arboreal, but several species spend much of their time in trees. For example, in species of *Conilurus* and *Mesembriomys*, the tail may be long and slightly bushy-tipped for balance. *Melomys* and *Uromys* species use their rather prehensile tail for gripping branches as they move. The former scurry along small branches whereas those of *Conilurus*, *Mesembriomys* and *Uromys* bound up the trunks and along the larger branches. A prehensile tail is well developed in *Pogonomys*.

Feeding and Digestive System

All species are essentially omnivorous with the bulk of the diet composed of plant material, mainly seeds or stems and some insect material (Watts 1977; Watts & Braithwaite 1978; Morton & Baynes 1985). Numerous partial exceptions are mentioned below.

Both the water rats are largely carnivorous, mainly eating invertebrates and fishes. Broad-toothed Rats (*Mastacomys fuscus*) and, to a much lesser extent, some species of *Rattus* and *Pseudomys* have developed broad molars and eat large amounts of grass and seed (Watts & Aslin 1981).

No anatomical studies have been done to correlate gut morphology with diet. The Greater stick-nest Rat (*Leporillus conditor*), which eats large quantities of green plant material (Watts & Eves 1976), has some anatomical and biochemical features of ruminants and further studies may reveal it has a stomach partially adapted to fermentation of plant material (Jones 1922; Robinson 1971).

The lower part of the gut of some Australian desert murids is thought to have particularly good water resorption capabilities, resulting in faeces that have a very low water content when the animal is water stressed (MacMillen & Lee 1969).

Lactating females of many species of Australian rodents, from xeric and mesic environments, ingest both urine and faeces from their young (Baverstock & Green 1975). The biological purpose of this behaviour, which occurs widely in mammals, is unknown.

Circulatory System

This conforms to the standard mammalian pattern. There is some indication that a heat-exchange counter-current system operates in the tail of the Water Rat.

Respiration

The effect of burrow-dwelling on respiration has been studied in Silky Mice (*Pseudomys apodemoides*) (Withers 1975, as *P. albocinereus*). This species constructs deep burrows in sand where concentrations of CO² are known to reach 9% and O² to fall to less than 20%. The respiratory response of this species to inspired CO² is similar to surface-dwelling rodents and, unlike some permanently fossorial rodents (Darden 1972; Withers 1975), shows no respiratory adaptation to burrow life. Baudinette (1972) found that oxygen consumption of burrow inhabitants was reduced by 18% in groups of animals when compared to single individuals.

Rates of pulmocutaneous water loss have been measured in a few Australian desert rodents and are rather high when compared to other desert animals (MacMillen & Lee 1970; MacMillen *et al.* 1971). In *Spinifex* Hopping-mice, water loss, mainly through respiration, can be reduced by up to 28% in groups of animals compared to single individuals (Baudinette 1972).

Excretion

Homeostasis of body fluids is regulated primarily through the kidney and secondarily through respiration, defecation and perspiration. Since many Australian rodents are found in desert regions, considerable attention has been given to regulation of electrolyte concentration and water balance physiology (MacMillen & Lee 1969, 1970; Collins & Bradshaw 1973; Baverstock & Watts 1974 and others). These studies show that many Australian desert rodents could exist on a diet of seed (without drinking water) and excrete metabolic by-products through the kidney using a minimum of water. Several species were capable of producing a urine with a mean osmotic pressure of up to 5000 mosmol. Urea was the major solute. *Spinifex* Hopping-mice can resorb renal water at the post-filtration stage (Hewitt, Baudinette & Wheldrake 1983) with the aid of highly elongated renal papillae (MacMillen & Lee 1969). The significance of interspecific variation in the ability to excrete urea and electrolytes is unclear (MacMillen & Lee 1969). Some, notably Long-haired (*Rattus villosissimus*) and Swamp (*R. lutreolus*) Rats, relinquish homeostatic control of some solutes and this presumably assists survival through temporary dry periods (Baverstock 1976b).

The neonatal kidney does not develop a regulatory function until close to weaning (Baverstock & Green 1975). Before this time, a dilute urine with a relatively constant concentration of salts is produced. When the mother-young unit is short of water, the recycling of water from the young to the mother is significant for the survival of the young. Approximately one-third of the water ingested from the mother's milk is returned to her, one-third is lost through evaporation and one-third remains in the young as it grows (Baverstock & Elhay 1979).

Excretion of unwanted exogenous materials (xenobiotics) that are lipophilic is much slower in the desert-dwelling *Spinifex* Hopping-mice than the laboratory mouse. Hydrophilic compounds, however, show few differences (Tonkin, Wheldrake & Baudinette 1977; Wheldrake, Hawke & Baudinette 1979). The difference in excretion of lipophilic compounds has been shown to be a function of lower rates of urine production in *Spinifex* Hopping-mice and not due to differences in metabolic processes in the liver (Wheldrake *et al.* 1979). The

excretion of the xenobiotic, phenol, by a range of Australian rodents has been studied by Baudinette *et al.* (1980). Few metabolites were identified (Phenyl glucuronide, Phenyl sulphate, Quinol glucuronide and Quinol sulphate). The proportions of these found in the urine varied considerably between species in an unexplained fashion.

Ingested solids not absorbed are excreted as solid pellet-form faeces. The rate of passage of these through the alimentary canal has not been measured accurately in Australian species, but is probably around 4–6 hours, similar to laboratory rats and mice.

Sense Organs and Nervous System

In Australian species no work has been done on olfaction, which is a major sensory input of environmental information in other rodents.

Neither has the hearing ability of Australian rodents been investigated. Studies of the vocalisations of *Notomys* species, Plain's Rats (*Pseudomys australis*) and *Rattus* species show that individuals of these species produce calls within a frequency range of 0.05–60 kHz with favoured ranges of 4–6 kHz and 20–30 kHz (Begg 1976; Watts 1975a, 1976, 1980). Their young produce calls in the 4–6 kHz and 30–60 kHz range (Watts 1975a, 1976, 1980). It is a reasonable assumption that these calls can be heard by adults and that their hearing is best at these frequencies.

The eyes of the Spinifex Hopping-mouse are proportionally much larger than those of the laboratory mouse and rat and have a predominance of rods (Smith 1976). The visual pathways of Spinifex Hopping-mice, Plain's and Long-haired Rats vary only slightly when compared to other rodents such as Brown Rats (*R. norvegicus*) (Mayner, Pearson & Sanderson 1980).

Long, sensory vibrissae are present on the heads of all Australian rodents, but no studies have been made of their exact function.

When first born, Australian rodents do not have fully developed sensory systems, although the general tactile and olfactory senses are well advanced (Happold 1976b). Full auditory ability does not develop until the external auditory meatus opens at an age of around 10–14 days (Happold 1976b). Before this time, a startle response to loud noises is apparent. Depending on the species, the eyes do not open until 7–21 days after birth (Watts & Aslin 1981).

The role of the pineal body has not been studied in Australian species, but it would be an interesting avenue to pursue in relation to breeding cycles and activity patterns.

Endocrine and Exocrine Systems

Breed (1978b, 1981a) has studied the relationship between progesterone levels and the female reproductive cycle. The Fawn-footed Melomys (*Melomys cervinipes*), which has a long oestrous cycle, has higher peripheral levels of progesterone than the Spinifex Hopping-mouse which has a short oestrous cycle. Studies of pregnant and lactating Spinifex Hopping-mice have shown that progesterone levels increase as the corpus luteum enlarges following implantation (Breed 1981a). The corpus luteum and luteal cells of the New Holland Mouse (*Pseudomys novaehollandiae*) enlarge during the latter half of pregnancy and a coincident increase in progesterone would be expected (Kemper 1977).

Studies of hormone levels of Bush Rats (*Rattus fuscipes*) living in natural populations (de Kretser *et al.* 1976) demonstrated that LH, FSH and testosterone are elevated in males during the breeding season. The relationships between breeding cycle, population size and hormone levels in free-living rodents needs to be studied more.

Exocrine glands are present in the form of specialised sebaceous glands in the chest, neck and chin of four species of *Notomys* (Watts 1975b). They are most active in adult males and pregnant or lactating females. Their function, although not known, is assumed to be related to scent-marking. In Brush-tailed Rabbit-rats (*Conilurus penicillatus*) there is an area of raised skin with associated vibrissae underneath the chin. In New Holland Mice, the superior parotid gland changes in activity, colour and size with reproductive condition (Kemper 1977).

The Harderian gland, which is thought to be involved in lubricating the eye, has been studied in Plain's Rat (Johnston *et al.* 1985). The gland and duct structure is not as complex as in African gerbils (*Meriones* species) which, like the Plain's Rat, are arid zone species.

Reproduction

The reproduction of Australian murids, particularly under laboratory conditions, is probably the most thoroughly studied aspect of their biology. In many respects the pattern is similar to that found in *Mus* and *Rattus*, but more studies probably will yield exceptions to the general rule. Reviews are found in Taylor & Horner (1973b), Watts (1974a, 1979b), Lee, Baverstock & Watts (1981) and Watts & Aslin (1981).

The anatomy and histology of the male reproductive system has been studied by several authors (Taylor 1961; Taylor & Horner 1970a, 1970b, 1971b, 1972, 1973b; Breed & Sarafis 1979, 1983; Breed 1980, 1981b, 1982b, 1983a, 1984). Table 47.1 lists the male accessory glands present in the different genera. All genera examined have vesicular, coagulating and prostate glands. *Conilurus*, *Mesembriomys* and *Melomys* lack preputial glands.

Table 47.1 Male accessory glands of Australian Muridae, by genus: * = present; - = absent; blank = unknown. (Data from various sources)

| GENUS | VESICULAR | COAGULATING | PROSTATE | BULBOURETHRAL | PREPUTIAL |
|---------------------|-----------|-------------|----------|---------------|-----------|
| <i>Rattus</i> | * | * | * | * | * |
| <i>Pseudomys</i> | * | * | * | * | * |
| <i>Leggadina</i> | * | * | * | | * |
| <i>Mastacomys</i> | | | | | |
| <i>Leporillus</i> | | | | | |
| <i>Notomys</i> | * | * | * | * | * |
| <i>Conilurus</i> | * | * | * | * | |
| <i>Mesembriomys</i> | * | * | * | | |
| <i>Melomys</i> | * | * | * | * | |
| <i>Uromys</i> | | | | | |
| <i>Hydromys</i> | * | * | * | | |
| <i>Xeromys</i> | | | | | |

The histology of the testis is similar to that in *Mus* and *Rattus* except in three species of *Pseudomys*, which have large amounts of interstitial tissue between the seminiferous tubules (Taylor & Horner 1970a; Breed 1982b). The genus *Notomys* (except the Fawn Hopping-mouse) is unusual in having very small testes and accessory glands (but a large ventral prostate) and a minute or absent copulatory plug in the female (Breed 1982b). The external morphology of the glans penis varies between species (Morrissey & Breed 1982).

The ventral hooks on the sperm head of most Australian Hydromyinae are unique within mammals (Breed 1983a, 1984). Interspecific variation exists in *Notomys* (Breed & Sarafis 1983) and *Pseudomys* (Breed 1983a). Some species have a pyriform or spatulate sperm head.

Species with limited breeding seasons (usually ones living in temperate regions) have testes and accessory glands which regress in the non-breeding period (Kemper 1980), although this is less pronounced in the genus *Rattus* (Taylor & Horner 1973b). Tropical species such as Large (*Zyzomys woodwardi*) and Common (*Z. argurus*) Rock-rats breed throughout the year and show no attrition of the male organs (Calaby & Taylor 1983).

Reproduction in the female has been well studied from the point of view of litter size, oestrous cycle, gestation length and post-partum oestrus (reviewed by Taylor & Horner 1973b; Watts & Aslin 1981). *Rattus* species have a short cycle of 4–7 days (Breed 1978a) with a post-partum oestrus, short gestation lengths of 21–24 days and a moderate litter size (means of four to eight). The Long-haired Rat has the highest reproductive potential. Non-*Rattus* species usually have reduced potentials with longer oestrous cycles (6–10 days) including a post-partum oestrus, longer gestation lengths (27–38 days) and smaller litters (one to four). Exceptions are the Western Chestnut Mouse (*Pseudomys nanus*), which is *Rattus*-like in many respects, the Long-tailed Mouse (***Pseudomys higginsii***), *Melomys* species, Large Rock-rats and Black-footed Tree-rats (*Mesembriomys gouldii*) which have long cycles and/or gestation lengths. Some species show evidence of delayed implantation during lactational pregnancies (Kemper 1976c; Breed 1979).

The histology of the ovary has not been studied in great detail, but it appears to be similar to that of the laboratory mouse and rat (Taylor & Horner 1970a, 1971b, 1973b; Kemper 1977; Breed 1977, 1981a). All Australian murids are thought to be spontaneous ovulators. The morphology and histology of the vagina and cervix show variation between species of *Pseudomys* and *Notomys* (Kemper 1977; Breed 1985). All five *Pseudomys* and one *Notomys* species studied have a duplex condition of the cervix, but in two *Notomys* species it is bicornuate with a narrow vaginal lumen. Breed (1985) commented on the complementary nature of the male/female reproductive characteristics of several of the Australian murids and their social systems.

The study of reproduction of Australian rodents in natural conditions is an area which requires much more attention, especially for arid zone species. Using museum specimens as a data base, Breed (1982a) concluded that there was no reproductive seasonality in Sandy Inland Mice (*Pseudomys hermannsburgensis*) and a slight increase in activity during the spring months in Spinifex Hopping-mice, but breeding could occur at any time of the year. Breed (1981c) also compared the latter with bipedal desert rodents in other parts of the world and concluded that wherever rainfall tended to be seasonal, breeding was also seasonal. In the Australian arid zone, reproduction (and sometimes plagues) may follow good rains (Finlayson 1939; Newsome & Corbett 1975). Laboratory studies suggest that water deprivation, short photoperiod and population density may reduce reproductive performance (Breed 1975, 1976).

Embryology, Development and Growth

Observations on embryo development have been made by Breed (1981a) for *Spinifex* Hopping-mice and Kemper (1976c) for New Holland Mice. Both species have a gestation length of 32 days when not prolonged by suckling. In the former, embryos move from the oviduct to the uterus on day five and implantation occurs on day seven when there are no suckling young, but is delayed up to day 18 when young are suckling. The mechanics of *Spinifex* Hopping-mouse embryo development and implantation were similar to that in the laboratory mouse although each cleavage stage took proportionately longer. The timing of these events appears to be similar in New Holland Mice.

Post-natal development is reviewed by Kemper (1976b), Fox (1979) and Watts & Aslin (1981). Some species develop rapidly (Table 47.2); they are furred, the incisors have erupted by or soon after birth, the pinnae are free and the eyes open at 7–12 days old (except in Long-tailed Mice, at about 15 days).

Table 47.2 Post-natal development rate and litter size in Australian murids. Values following species names are mean litter sizes, ranges in parentheses. Data from many sources. * = $p < 0.05$; *** = $p < 0.001$; P. = *Pseudomys*; Mes. = *Mesembriomys*; Mel. = *Melomys*; L. = *Leporillus*; Ma. = *Mastacomys*; C. = *Conilurus*; H. = *Hydromys*; N. = *Notomys*; R. = *Rattus*.

| RAPID DEVELOPERS | MODERATE DEVELOPERS | SLOW DEVELOPERS |
|--|---|---|
| <i>P. gracilicaudatus</i> 2.4 (1-4) <i>P. higginsii</i> 3.1 (2-4) <i>Mes. gouldii</i> 1.8 (1-3) <i>Mel. cervinipes</i> 1.8 (1-3) <i>Mel. burtoni</i> 2.8 (1-5) <i>L. conditor</i> 2 <i>Ma. fuscus</i> 2.0 (1-3) <i>C. penicillatus</i> 2.8 (1-4) | <i>P. novaehollandiae</i> 4.0 (1-6) <i>P. pilligaensis</i> 4.0 (3-5) <i>P. australis</i> 3.6 (1-7) <i>P. desertor</i> 3.0 (1-4) <i>P. apodermoides</i> 3.8 (3-7) <i>P. praeconis</i> 3.5 (3-4) <i>P. delicatulus</i> 2.5 (3-4) <i>H. chrysogaster</i> 3.29 (1-7) | <i>N. alexis</i> 4.0 (1-9) <i>N. cervinus</i> 3.5 (2-4) <i>N. mitchellii</i> 3.6 (2-5) <i>R. fuscipes</i> 4.2 (2-6) <i>R. villosissimus</i> 8.3 (5-10) <i>R. sordidus</i> 6.0 (3-14) <i>R. lutreolus</i> 3.8 (1-6) |
| <div style="display: flex; justify-content: space-between; align-items: flex-start;"> <div style="text-align: center;"> <p>x Litter Size 2.27</p> <p>Range: 1-5</p> <p>***t=4.177</p> </div> <div style="text-align: center;"> <p>3.63</p> <p>1-7</p> <p>*t=1.833</p> </div> <div style="text-align: center;"> <p>4.77</p> <p>1-14</p> <p>***t=3.732</p> </div> </div> | | |

At the other end of the scale are species that develop slowly. They do not have a dense pelage until at least 2 weeks old, the incisors erupt at 6–16 days (except in *Spinifex* Hopping-mice at 2–3 days) and the eyes open at 16–28 days. Other species are intermediate between these two extremes.

When litter size is compared with rate of development, there is a clear difference between rapidly developing species and others (Table 47.2). Mean litter size is significantly smaller in the rapid, compared to moderate and slow groups, but there is no difference between moderate and slow groups. If litter sizes were

small, more intrauterine resources should be available per individual embryo resulting in more development. This also may be the reason why birth weight, as a proportion of adult weight, is greater in species with small litter sizes (Fig. 47.3). The length of gestation does not appear to influence the rate of development. Both Eastern Chestnut Mice (*Pseudomys gracilicaudatus*) and Black-footed Tree-rats are rapid developers, yet the first has a gestation of 27 days (Fox & Kemper 1982; Fox 1983b) and the second, 44 days (Crichton 1969).

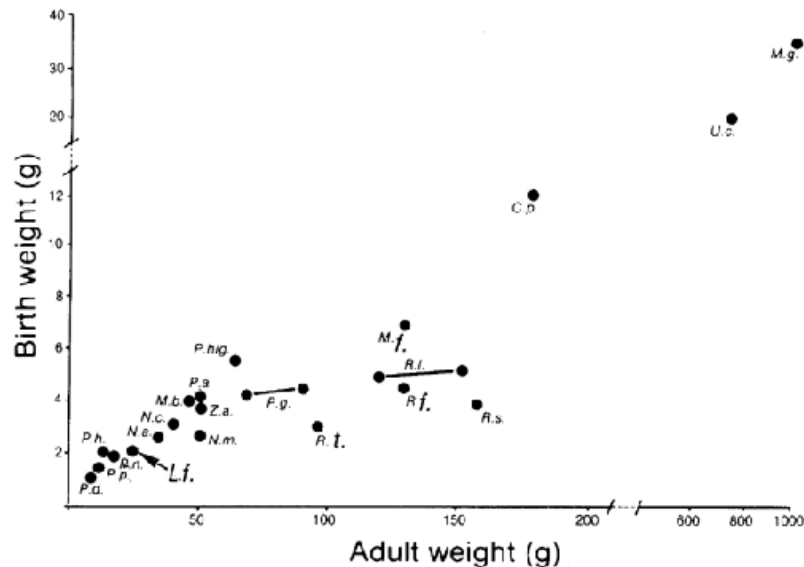


Figure 47.3 Birth weight in relation to adult weight for 20 species of Australian murid. Data from many sources. P.d., *Pseudomys delicatulus*; P.p., *Pseudomys pilligaensis*; P.n., *P. novaehollandiae*; P.h., *P. hermannsburgensis*; L.f.: *Leggadina forresti*; P.hig., *P. higgins*; P.g.: *P. gracilicaudatus*; P.a., *P. australis*; N.a., *Notomys alexis*; N.c., *N. cervinus*; N.m., *N. mitchellii*; Z.a., *Zygomys argurus*; M.f., *Mastocomys fuscus*; C.p., *Conilurus penicillatus*; R.l., *Rattus lutreolus*; R.f., *R. fuscipes*; R.s., *R. sordidus*; R.t., *R. tunneyi*; U.c., *Uromys caudimaculatus*; M.g., *Mesembriomys gouldii*.

A natal pelage (or in a few instances, a juvenile pelage) is present at birth in all species. It is very sparse and fine and is replaced later by a juvenile pelage or true fur which is softer, greyer and less dense than the adult. A post-juvenile moult has been reported in New Holland Mice (Kemper 1976a) which begins on the ventral surface at about 5–6 weeks of age and is complete by about 14 weeks. It also occurs in Eastern Chestnut Mice (Fox & Kemper 1982), Water Rats (Olsen 1983) and Brush-tailed Rabbit-rats with roughly the same timing.

Sexual maturity, including gonadal maturation, has been studied in Bush Rats (Taylor & Horner 1971a), and with minor variations, is similar to the laboratory rat. Vaginal perforation precedes the first ovulation by about 1 month in *Rattus* species. In New Holland Mice and probably many other non-*Rattus* species, vaginal perforation is followed very quickly by oestrus detected by either cornification or mating (Breed 1979; Kemper 1976c). The age at which sexual maturity takes place is generally greater in males than in females and less in *Rattus* than non-*Rattus* species (Watts 1979b). Most *Rattus* species mature, at least in the laboratory, at 1–3 months of age and most other species at 2–5 months (Smith *et al.* 1971; Kemper 1976c; Watts 1979b). In natural populations, maturation usually is delayed until the following breeding season (see Life History).

Post-natal growth of Australian murids has been reviewed by Kemper (1976c) and Fox (1979) with several additional species discussed by Watts (1979a). Many species are sexually dimorphic with males the larger, but Breed (1983b) noted that the reverse is the case with *Spinifex* Hopping-mice. There appears to be no relationship between adult size and the rate of growth, with most species reaching adult or near-adult size by the time they are 3–4 months old. Information available for New Holland Mice living in the wild shows that individuals born early in the breeding season grow quickly with growth rates similar to laboratory-raised animals (Kemper 1979). Individuals born later in the breeding season grow more slowly and do not reach maximum size until the next breeding season.

In the early stages of growth, body weight changes are multiphasic (Kemper 1976b; Fox 1979; Fox & Kemper 1982). Decreases in growth rate are noted at the time of eye opening and weaning that may be due to changes in activity and food intake in the young animals. Experimental studies are needed to confirm this.

In all species of the Conilurini and Uromyini studied, the neonates cling tightly to the teats of their mother for the first days or weeks while both are in the nest. Young of *Rattus* and Hydromyini do not show this behaviour. Milk composition varies depending on the time since parturition, number of young and water balance of the mother-young unit. Peak lactation tends to occur about 10 days after birth when the milk consists of 30% total solids, 15% fat, 6% protein and 3% sugar although there is appreciable variation between species. When water intake is reduced, less, more concentrated, milk is produced, growth rate of the young is reduced and lactation extended (Baverstock & Watts 1975).

NATURAL HISTORY

Life History

Life history information is available for about 16 species of Australian murid (Table 47.3), although for some it is far from complete. With the exception of the Long-haired Rat, no arid zone species has been studied in detail. The life histories of inland rodents are of particular interest because some species exhibit periodic population densities of plague proportions.

Species in the genus *Rattus* have a higher reproductive potential than other Australian murids (see Reproduction), and so it might be expected that *Rattus* species would have life histories involving short lifespans, high annual population turnover and early sexual maturation. Certainly, all are apparently capable of breeding in their season of birth (Taylor & Horner, 1973b). As yet, only one population of Swamp Rats (a commensal one) has been shown to have a substantial proportion of females mature early (Braithwaite 1980a). In natural habitats, this species lives longer and rarely breeds early (Table 47.3). In most wild *Rattus* the maximum longevity is 1–2 years.

Life histories of *Pseudomys* species are variable. Cockburn, Braithwaite & Lee (1981) reviewed those living in fire-perturbed habitats in south-eastern Australia and concluded that there are three basic patterns: 1) year-round breeding populations; 2) populations in which individuals only breed in one season; and 3) populations which breed over more than 1 year.

Interestingly, three of the species discussed could utilise two different patterns depending on the habitat occupied. Like *Rattus* species, some species can breed in their season of birth. For instance, New Holland Mice in the wild can be mature as young as 7 weeks old (Kemper 1980). Maximum longevity is seen in Smoky Mice (*Pseudomys fumeus*) and Heath Rats (*Pseudomys shortridgei*).

Common and Large Rock-rats (Begg 1981c, 1983a, 1983b) live less than 2 years and reproduce in their first breeding season. There is some evidence that *Melomys* species may live 2–3 years in certain situations (Smith 1985; Wood 1971).

Table 47.3 The life history strategies of some Australian rodents. Data are from field studies; first season = breeding season of birth; R. = *Rattus*; P. = *Pseudomys*.

| Species | Longevity | Survival | Sexual Maturity | Reference |
|---|-------------------------------------|---|---|--|
| <i>R. fuscipes</i> | Average = 12 mths ≤ 1 year | Juv. - ♀ > ♂ 1:1 ♂ > ♀ | Some ♂ + ♀ in first season | Warneke (1971) Taylor (1961) |
| <i>R. lutreolus</i> heath | 1-2 years | ♀ > ♂ | ♂ never in first year ♀ rarely in first year | Braithwaite & Less (1979) |
| commensal | 13 months | ♀ > ♂ | ♀ many in first year | Braithwaite (1980) |
| <i>R. sordidus</i> | 3 years ≤ 2 years | | ♂ ≥ 5 months ♀ ≥ 2 months | McDougall ('946) Gard (1935) |
| <i>R. colletti</i> | | ♀ > ♂ | Some in first season 4-6 weeks | Redhead (1979) Gard (1935) |
| <i>R. villosissimus</i> | ≤ 18 months | ♂ > ♀ | ≥ 3 months | Carstairs (1975) |
| <i>P. novaehollandiae</i> | ≤ 2 years | ♀ > ♂ | ≥ 7 weeks Some in first season | Kemper ('980, '977) |
| <i>P. apodemoides</i> | ≤ 2 years | ♀ > ♂ during breeding | Some in first season | Cockburn (1981a) |
| <i>P. fumeus</i> | > 2 years | ♀ > ♂ | None breed in first season | Cockburn (1981b) |
| <i>P. shortridgei</i> Mature heath Regenerating heath Exposed dune | 2-3 years ≤ 2 years 2-3 years | Adult > Juv. Juv > Adult Adult > Juv. | Second season First season Second season | Cockburn <i>et al.</i> (1981) |
| <i>P. higginsii</i> | ≤ 18 months | | | Green (1983) |
| <i>P. gracilicaudatus</i> | < 18 months | Juv. > Adult | Some in first season | Fox (1983, pers. comm.) |
| <i>Zyzomys argurus</i> | ≤ 2 years | ♂ > ♀ | 5-6 months | Begg (1980) |
| <i>Zyzomys woodwardi</i> | ≤ 2 years | ♀ > ♂ | 5-6 months | Begg (1981) |
| <i>Hydromys chrysogaster</i> | | ♂ > ♀ | Some ♀ at 4 months Most ♀ at 8 months | McNally (1980) Olsen (1983) |
| <i>Melomys cervinipes</i> | < 2½ years | ♂ = ♀ | Some ♀ breed in first season | Wood (1971) Smith (1985) |
| <i>Melomys burtoni</i> Mangrove Vine thicket | > 2 years ≤ 1 year > 1½ years | ♂ = ♀ ♀ > ♂ | Late Early | How (pers. comm.) Begg <i>et al.</i> (1983) |

Survival is usually greater in females than in males (Table 47.3), especially during the breeding season. Exceptions are found in Common Rock-rats, Long-haired and Water Rats.

Ecology

Early accounts of Australian rodent 'ecology' described the natural history of species using specimens obtained mostly from Aborigines and local European residents. This is all that is known of the ecology of some arid zone species that are now extinct or rare. From studies in the past 15 years, a good deal is known about the population dynamics and habitat preferences of four species of *Rattus*, five *Pseudomys*, two *Zyzomys*, one *Mesembriomys*, two *Melomys*, *Hydromys* and *Mus*. Most of the studies are the same as those referred to in Table 47.3.

Population fluctuations of Australian murids tend to fall into three categories:

Annual cycles are typical of coastal, seasonally breeding species. This pattern occurs in most species of the eastern, south-eastern and south-western seaboard, no doubt due to favourable conditions in spring and summer in these regions. Lowest population numbers occur in late winter and early spring and peak populations are found in autumn. Some species in the wet/dry tropics have annual cycles which are more prolonged than their southern counterparts.

Non-cyclical fluctuations of arid zone species have received very little attention and are much in need of long-term study. Numbers of some species are known to fluctuate markedly, so much so that they 'disappear' from areas for years at a time (Newsome & Corbett 1975; Watts & Aslin 1981).

Some tropical murids have relatively stable population densities throughout the year (Begg *et al.* 1983; Kemper *et al.* 1987), but fluctuations can occur between years (Friend 1987). This pattern is due, in part, to more prolonged or year-round recruitment of young.

In some arid zone species, spectacular outbreaks in numbers (plagues) occur. Newsome & Corbett (1975), Saunders & Giles (1977) and Chapman (1981) reviewed the literature pertaining to rodent plagues in Australia, including those of the introduced *Mus*, and concluded that the vast variation in rodent numbers is due to a fluctuating food supply and changes in predation pressure. In addition to the arid zone species, at least two species of the wet/dry tropical grasslands, Dusky (*Rattus colletti*) and Canefield (*R. sordidus*) Rats, can reach very high densities (McDougall 1946; Redhead 1979).

The age structure of populations is related to the breeding pattern of the species. In those that have a defined breeding season, there is a high proportion of juveniles near the end of and just after breeding (Kemper 1977; Begg 1981c; Cockburn 1981a, 1981b; Cockburn *et al.* 1981). In many species, this juvenile cohort forms the entire breeding contribution to the early part of the next breeding season. Tropical species with year-round breeding, such as the Grassland Melomys (*Melomys burtoni*), have a more even age distribution throughout the year (Begg *et al.* 1983; Kemper *et al.* 1987). With the exception of some studies of *Mus* (Newsome & Crowcroft 1971) and Long-haired Rats (Carstairs 1976), nothing is known of the age structure of populations during plagues.

Movements of individuals are usually reported as the average distance between captures. Males generally move further than females and adults move further than juveniles except during dispersal. For adults of all species studied, the average distance moved ranges is about 15–170 m, but may vary intraspecifically depending on habitat and population density. As density increases, mean distance decreases (Braithwaite & Lee 1979; Barry 1984). Dispersals of greater than 1 km have been noted in Bush Rats (Warneke 1971). Home range size (in terms of area occupied) has been determined only for New Holland and Eastern Chestnut Mice, Large and Common Rock-rats, and is less than 0.5 ha (Kemper 1977; Fox 1981; Begg *et al.* 1983).

Whether any Australian murid is truly territorial is unknown. Most species appear to have social systems which allow overlap in home ranges, particularly between females and males. Several species of *Pseudomys* and *Notomys* live in groups of a few to many individuals (Watts & Aslin 1981) that would presumably hold group territories or home ranges. Tail scarring has been used in several studies as a measure of fighting within a population (Braithwaite & Lee 1979; Braithwaite 1980b; Cockburn 1981b; Cockburn *et al.* 1981). Differences between seasons were apparent.

Recent studies of habitat selection by Australian murids have highlighted the relationship between disturbance, particularly fire, and recolonisation by suites of species. In temperate Australia, *Mus* and many *Pseudomys* species are adapted to early and mid-successional stages, and *Rattus* species prefer older successional stages (Braithwaite & Gullan 1978; Cockburn 1978; Fox & Fox 1978, 1984; Fox & McKay 1981; Cockburn *et al.* 1981, 1983a; Fox 1982c, 1983a). Important factors in determining habitat selection are: floristic composition, structure of vegetation, food availability and shelter. Few studies on the effects of fire on rodent populations in the tropical grasslands and

woodlands have been done (Begg, Martin & Price 1981; Kerle & Burgmann 1984). Studies of this relationship in such a fire-perturbed environment would prove most interesting.

Introduced rodents, especially *Mus*, species have been blamed for the demise of native species (Newsome & Corbett 1975) because they are often abundant where native species are scarce. However, evidence suggests that the opposite may be true in some cases (for example, New Holland Mice and *Mus*; Cockburn 1980), or at least that no deleterious effects are obvious even during *Mus* plagues (Chapman 1981). Interactions between native species have been studied in only a few cases. Fox (1981) noted three possible pairs of interacting species in a coastal heathland community, two of which shared the same food niche, one showing temporal separation in the habitat succession and the other reciprocal abundance and habitat shifts. Most encounters in the laboratory between the Black (*Rattus rattus*), Swamp and Bush Rats were amicable, but in those cases where they were agonistic, Black Rats were usually dominant over Swamp Rats (Braithwaite 1980b).

Several Australian predators are known to include rodents in their diet, but amounts vary greatly depending on habitat, predator species and rodent abundance. Dingoes take more rodents, particularly Long-haired Rats, during plagues (Newsome & Corbett 1975) than at other times when they mainly eat medium to large-sized prey (Whitehouse 1977; Newsome *et al.* 1983b; Robertshaw & Harden 1985a). In general, rabbits, sheep and *Mus* are the most important prey items of foxes. In alpine New South Wales, selective predation by foxes occurs on Broad Toothed Rats, especially during winter (Green & Osborne 1981). Feral cats have been suggested as important predators of native rodents, but again this may depend on the region studied. In arid areas, rabbits and *Mus* species make up a large proportion of the diet (Bayly 1976; Jones & Coman 1981). In montane forests, the proportion (by weight) was much higher (40%), the abundant Bush Rat making up a substantial part of their diet. Studies of owl diets in Australia have shown rodents to be the most important prey items (Morton *et al.* 1977; Morton & Martin 1979), the proportion of each species taken depending on its abundance at the time.

Studies of predator diets in Australia have been greatly facilitated by hair identification guides (Brunner & Coman 1974).

The study of murid/parasite interactions in Australia is in its infancy. Most of the literature deals with descriptions of new parasite taxa or surveys of the parasites which occur in a few rodent species. In a review of the records of internal parasites of Australian mammals, Mackerras (1958) listed species from the introduced rodents (which have the same parasites as elsewhere in the world) as well as Bush, Canefield, Water, White-tailed (*Uromys caudimaculatus*), and Long-haired Rats, and Fawn-footed and Grassland (*M. burtoni*) Melomys. Since the publication of that catalogue, more work has been carried out on the Water Rats (Beveridge 1980b; Obendorf & Smales 1985), Bush Rat (Obendorf 1979) and *Mus* (Singleton 1985). About 70 new records of parasites of Australian murids have been documented, but only one new host, the Swamp Rat, has been studied (Beveridge personal communication). Only studies by How *et al.* (1983) and Singleton (1985) investigated seasonal and habitat changes in parasite loadings in natural populations. Other relevant papers on internal parasites include those reviewing or surveying pentastomid arthropods (Riley, Spratt & Presidente 1985) and the sporozoan *Sarcocystis* (Munday *et al.* 1978). *Leptospira* has also been recorded (Durfee & Presidente 1979). Some notes on ectoparasites are given by Robinson *et al.* (1978) and Domrow (for example, 1978a, 1978b).

Fleas from Australian rodents have been studied by Traub (1972) and Dunnet & Marden (1974). The fauna is a mixture of endemic and cosmopolitan taxa, with several of the cosmopolitan species thought to have been introduced along with their host. It has been suggested that several flea groups arose in Australia and have spread north into South-east Asia rather than the more usual route in the opposite direction (Traub 1972).

Behaviour

Happold (1976a, 1976b) provided detailed information on behaviour in captivity and general ontogeny of four species of Conilurini. Unlike desert rodents of other continents, Australian species can be highly social, for example, *Spinifex* Hopping-mice tend to form small colonies from which strange individuals are physically excluded. Food hoarding behaviour has not been recorded in any Australian species.

Specific behaviours have been noted in Australian murids. The Greater Stick-nest Rat uses interwoven sticks to build large complex nests that each contain several occupants, each cooperatively building and defending it (Aslin 1972). The False Water Rat is adept in using its forefeet and mouth to construct burrows and nests in the mud around mangrove roots. These burrow systems are plugged at high tide, thus avoiding inundation (Magnusson, Webb & Taylor 1976). Freshwater mussels are placed by the Water Rat on sunny river banks to dry and open, thus allowing easy access to the contents (Barrow 1964). Protective paternal behaviour has been noted only in *Notomys* and Bush Rats (Horner & Taylor 1969; Happold 1976b).

Economic Significance

The deleterious effects of the activities of Australian murids are relatively few when compared to the amount of damage done by the introduced species. Some species in the genus *Rattus* and *Melomys* have been reported to cause damage to rice crops, sugar cane and forest plantations (McDougall 1944a, 1944b; McNally 1955; Taylor & Horner 1973b). The burrows of Water Rats in levee banks of irrigation schemes are a minor nuisance. Species of *Rattus* can harbour *Leptospira*, the causative agent of leptospirosis which can infect humans, particularly during manual harvest of sugar cane (Sawers 1938).

The introduced murids, House Mice (*Mus domesticus*) and Black and Brown Rats, are responsible for damage costing hundreds of millions of dollars throughout Australia due to spoilage of stored grain. Brown Rats are confined to coastal cities and ports where they do considerable damage to stored products.

Some Australian species, such as *Spinifex* Hopping-mice and Plain's Rat, have been domesticated and now are widely distributed as pets, laboratory animals and educational subjects (Baverstock 1980). Attempts to domesticate other species of Australian rodents have been made with varying success (Watts 1982a, 1982b). The Water Rat, once widely hunted for its luxurious pelt, is now protected (Watts & Aslin 1981).

Eight species of Australian rodent are known to have become extinct and many others suffered range reductions since European settlement (Watts 1978). This has been most marked in the arid and semi-arid regions (Morton & Baynes 1985). All species now are protected from indiscriminate capture by legislation. The conservation status of all species is reviewed by Watts (1984).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Murids are found throughout Australia. Present day concentrations of species (nine to 12) are in Cape York, northern coastal New South Wales, the Kimberley and Arnhem Land. At the other end of the scale, many parts of the arid zone have only two to three species (Lee *et al.* 1981; Watts & Aslin 1981; Morton & Baynes 1985). Recent studies of subfossil bone deposits estimated to be 100–200 years old show that the modern picture bears little relationship to the pre-European situation (Smith 1977; Baynes 1984; Morton & Baynes 1985; Watts & Ling 1985). The deposits show that many more species (4–13, depending on area) once occurred there. The only modern glimpse of this faunal assemblage is through the collections made in central Australia late in the 19th Century when twelve species of rodents were recorded, five of which are now extinct in that area (Watts & Aslin 1981; Morton & Baynes 1985).

What are the limiting factors in the distribution of Australian murids? Fox (1985) found that in the temperate heathlands and forests of south-eastern Australia the basic rodent community consisted of one *Rattus* and one *Pseudomys/Mastacomys* species. Additional resources allowed more species in any particular area and habitat diversity was considered important in determining this. In tropical Australia, increasing habitat structural complexity, floristic richness and greater food resources was associated with higher species richness of mammals (Braithwaite *et al.* 1985). Since structural complexity is greater in the forests and woodlands of the north when compared to the arid zone, the larger number of species in the tropics is expected. Because representatives from both faunas are often present, the boundary regions between arid zone and tropical or southern coastal areas have more species than the central arid zone (Morton & Baynes 1985).

The taxonomic groups of Muridae in the Australian Region (see Classification) have different geographic distributions (Table 47.4). Members of the Conilurini are widespread across the continent, but occur only marginally in Papua New Guinea. The Uromyini is restricted to wetter areas of the northern and eastern coasts as far south as central, coastal New South Wales. The Hydromyini is restricted to aquatic or near aquatic environments throughout Australia except the central Australian drainage basin. The Uromyini and Hydromyini are well represented in Papua New Guinea (Menzies & Dennis 1979). The native Murinae are predominantly animals of the wetter coastal fringes. Two species, the Long-haired Rat and the Pale Field-rat (*R. tunneyi*), have (or had in the case of the latter) a much wider distribution in inland Australia (Watts & Aslin 1981). The Murinae is found throughout the Old World, but apart from introductions, is unknown in the New World. The introduced House Mouse has adapted well to Australian conditions and now is found throughout most of the continent. In contrast, the introduced Black and Brown Rats are restricted to coastal regions (Watts & Aslin 1981).

Affinities with other Groups

The phylogenetic affinities of Australian Murinae are clearly with congeners in New Guinea and South-east Asia (Taylor & Horner 1973a), but the affinities of the Hydromyinae are more obscure. There are strong relationships with the Papua New Guinea fauna that, with the possible exception of one or two genera, should be considered as an integral part of a radiation in the Australian Region. *Hydromys*, *Uromys*, *Melomys* and *Pogonomys* all have congeners in Papua New Guinea and *Xeromys* is closely related to the small Papua New Guinea Hydromyini such as *Mayermys* and *Pseudohydromys* (Tate 1951a). How this

Table 47.4 The classification and distribution of Australian Muridae; intro. = introduced

| SUBFAMILY AND TRIBE | GENUS | DISTRIBUTION |
|---------------------|---|---|
| Murinae | <i>Rattus</i> | Australia New Guinea Asia |
| | <i>Mus</i> | Australia (intro.) New Guinea (intro.) Asia Africa Europe |
| | +104 other genera throughout the Old World (Honacki <i>et al.</i> 1982) | |
| Hydromyinae | | |
| Hydromini | <i>Xeromys</i> | Australia |
| | <i>Hydromys</i> | Australia New Guinea |
| | +8 other genera in New Guinea | |
| Uromyini | <i>Uromys</i> | Australia New Guinea |
| | <i>Melomys</i> | Australia New Guinea Indonesia |
| | +3 other genera in Papua New Guinea and Solomon Islands | |
| Uncertain | <i>Pogonomys</i> | Australia New Guinea |
| | +6 other genera in New Guinea | |
| Conilurini | <i>Conilurus</i> | Australia Papua New Guinea |
| | <i>Mesembriomys</i> | Australia |
| | <i>Zyzomys</i> | Australia |
| | <i>Notomys</i> | Australia |
| | <i>Pseudomys</i> | Australia Papua New Guinea |
| | <i>Mastacomys</i> | Australia |
| | <i>Leporillus</i> | Australia |
| | <i>Leggadina</i> | Australia |

radiation is related to the murids of South-east Asia is unknown. The nearest relatives may be some unusual genera in the Philippines (*Crunomys*, *Rhynchomys*) and Sulawesi (*Echiothrix*) which share with some Australian and New Guinea genera a lower complexity and number of molars (Misonne 1969). Studies on albumin evolution in murids suggest that the Hydromyinae is an early offshoot of a *Rattus*-like radiation that took place in the Miocene in South-east Asia (Watts & Aslin 1981).

Affinities within Australian Muridae

Affinities within Australian *Rattus* (Murinae) have been studied extensively (Taylor & Horner 1973a; Baverstock, Watts & Hogarth 1977a; Baverstock *et al.* 1981; Baverstock *et al.* 1983c). Body structure, chromosomes and biochemistry all indicate a close relationship between Long-haired, Canefield and Dusky Rats (often called the Canefield Rat group). The Pale Field-rat is a more distant member of this group. The other three *Rattus* species appear to be equally distant from each other and the Canefield Rat group.

Affinities within the Australian Hydromyinae) also have been well studied (Baverstock *et al.* 1977b, 1980, 1981, 1983c; Breed 1984) (Table 47.4). Hydromys and Xeromys, both members of the Hydromyini, are only distantly related to each other whereas *Uromys* and *Melomys* (Uromyini) are quite closely related. The Conilurini comprises eight genera. Of these, *Mesembriomys*, *Conilurus* and *Zyzomys* appear to be monophyletic. The same applies to *Pseudomys*, *Mastacomys* and, possibly, *Leporillus*. *Notomys* appears to be an early offshoot of this latter group. The genus *Leggadina*, previously considered congeneric with *Pseudomys*, is an isolated lineage.

Preliminary estimation of the time of origin of the Hydromyinae is around 15 mybp. The major lineages (tribes) within the subfamily seem to have arisen around 10 mybp (Watts & Aslin 1981; Sarich 1985).

Even though there is no supporting or refuting fossil evidence, there is a general impression based on the modern distribution of genera, that the basic radiation within the Conilurini took place mainly in the drier areas of Australia, whereas that of Uromyini and Hydromyini took place in the tropical, forested areas of an Australian/New Guinea land mass. An alternative is that the Uromyini and Hydromyini arose within the widespread rainforests of late Miocene Australia and their present distribution is essentially a relict one.

Within the Conilurini there is evidence, based on the distribution of closely related species, that the semi-arid zone has been the main area of recent species diversification (Baverstock 1982b). Similar considerations of *Rattus* show that the intermittent barrier of Torres Strait has had a role in the evolution of some modern species (Taylor, Calaby & Smith 1984).

Fossil Record

Fossil and sub-fossil rodents are plentiful in deposits in southern and eastern Australia from some 40 000 years ago onwards (Hand 1984a). These represent modern species except for two (as yet undescribed), one in *Pseudomys* and one in *Notomys* (Watts & Aslin 1981).

In deposits which are older than 40 000 years, rodent fossils are sparse. The earliest are from the Bluff Downs and Chinchilla deposits in Queensland and date back to 4–4.5 mybp. They are represented by an incisor and a few molar teeth, respectively, which have yet to be described (Hand 1984a). The earliest murid fossils yet discovered are from the Middle Miocene of northern Pakistan, by which time at least two lineages were well established (Jacobs 1977).

COLLECTION, PRESERVATION AND LABORATORY CULTURE

Collection and Preservation

The general techniques of collection and preservation of mammal specimens are described in DeBlase & Martin (1974) and Nagorsen & Peterson (1980). Watts & Aslin (1981) discuss the particular case of Australian rodents.

European and North American methods of trapping small mammals do not always yield the best results in the Australian situation, particularly in the arid zone. How, Humphreys & Dell (1984) reviewed studies comparing trapping techniques in Australia with their own results in arid and semi-arid Western Australia. They concluded that pitfall traps were more successful in arid habitats than snap traps or box traps. The most effective surveys are those which utilise a variety of methods.

There are no major differences between preservation techniques in Australia and elsewhere except that it has, perhaps, taken longer to educate museums to fix in formalin before preserving in ethanol. In some institutions, traditional museum techniques have been supplemented with newer methods such as frozen tissue collections for biochemical analysis. This is especially useful for identifying some of the smaller *Pseudomys* where morphological determinations are difficult.

Laboratory Culture

With few exceptions, Australian murids are kept easily in captivity in conditions similar to those generally used for laboratory mice. Larger species such as *Hydromys*, *Uromys* and *Mesembriomys* require more spacious accommodation and provision made for their gnawing abilities. Some, such as *Hydromys*, *Xeromys*, *Mastacomys* and *Leporillus*, require specialised diets. Others such as *Melomys* and *Zyzomys* are aggressive and may need to be housed individually. Husbandry details for most species are given in Watts (1982a). As mentioned earlier, several species, notably the Spinifex Hopping-mouse and Plain's Rat, have adapted well to captivity and are becoming quite common in educational institutions (Baverstock 1980).

Other than the introduced species, all rodents in Australia are protected by law and permits from State Wildlife Authorities are required before they can be collected from the wild or kept in captivity.

GENERIC DESCRIPTIONS

Rattus

(Weight 100-300 g) True Rats

True rats are closely related to congeneric species in New Guinea and South-east Asia (Taylor *et al.* 1984) and are believed to have arrived in Australia/New Guinea about 1 million years ago (Simpson 1961; Watts & Aslin 1981).

Rattus species are often the most abundant rodents in coastal areas. The Polynesian Rat (*R. exulans*), is widespread in South-east Asia, but known from only two offshore islands in Australia. The Long-haired Rat periodically plagues over a vast area of inland Australia following good seasons (Plomley 1972), but other times it is rare and restricted to small scattered areas of permanent water along creeks and bore drains. Many of the species are known to hybridise in the laboratory, but no instance of hybridisation in the wild is known (Fox & Murray 1979; Baverstock *et al.* 1983c).

Mus

(Weight 15-30 g) House Mouse

The taxonomy of *Mus* in Australia is uncertain due to new evidence from Europe that several species occur there and could have contributed to the gene pool of introduced *Mus* in Australia (Marshall & Sage 1981; Thaler, Bonhomme & Britton-Davidian 1981). We take the view that it is probably *M. domesticus*, not *M. musculus*, that was introduced here, but further studies are needed to clarify this point.

House Mice were introduced early in European settlement or possibly earlier (Hand 1984a). Wild mice occur in plague proportions at times in agricultural areas of southern Australia. They also can reach high densities after good seasons in central Australia (Newsome & Corbett 1975; Saunders & Giles 1977). The House Mouse has a very opportunistic diet, the composition or

which ranges from all insect to all plant (Watts 1970; Watts & Morton 1983). In his (1982) study of fire disturbed habitats, Fox found that the diet varied according to habitat and what other rodents were present. In general, the House Mouse is one of the first species to recolonise an area after a fire, reaching peak abundance about one year after a fire, then becoming very scarce. Its appearance in some habitats may be delayed (Fox 1982c).

Uromys

(Weight 600-800 g) White-tailed Rat

The White-tailed Rat is one of the largest rodents in Australia. It is arboreal and probably lives a solitary life on a diet of seeds and nuts (Wellesley-Whitehouse 1983).

Captive colonies have been relatively successful and individuals have lived for over 6 years. If tamed from before weaning, they make gentle pets. Two chromosome races exist on Cape York. The northern race has chromosomes with extensive areas of heterochromatin. The chromosomes of the southern race lack these but have a variable number of small supernumerary chromosomes (B chromosomes) (Baverstock 1976a; Baverstock, Gelder & Jahnke 1982b).

Melomys

(Weight 25-165 g) Mosaic-tailed Rats

The *Melomys* genus extends to Halmahera (Moluccas), making it the most westerly member of the Hydromyinae. Detailed studies of chromosomes and biochemistry have helped to clarify a previously confused taxonomy in Australia (Baverstock *et al.* 1980), but morphological studies are needed to complete the picture. In Australia, four species are now recognised. They are restricted to the forested and grassland areas of the north and east of the continent (Watts & Aslin 1981). One species, Thornton Peak *Melomys* (*Melomys hadrourus*), is known only from two mountain peaks in northern Queensland (Winter 1984b). *Melomys* species are aggressive towards each other in captivity, implying a solitary existence in the wild. In agricultural crops such as sugar cane, densities can become quite high and result in extensive crop damage (McDougall 1944a).

Pogonomys

(Weight 50-70 g) Prehensile-tailed Rat

Studies on the karyotype and body morphology of *Pogonomys* (Menzies & Dennis 1979) place it in the Hydromyinae, but its tribal position is unclear. Several species are known from New Guinea, but only one, the Prehensile-tailed Rat (*P. mollipilosus*), occurs in Australia. It is restricted to two or three areas of rainforest on Cape York. These populations may be relicts of the time when eastern Cape York and New Guinea were joined and more extensively forested. It is the only Australian non-*Rattus* species with more than two pairs of mammae ($2 + 1 = 6$).

Hydromys

(Weight 600-1300 g) Water Rat

One morphologically variable species, the Water Rat, occurs in Australia. It is widespread in coastal regions and some inland waterways and it and two other species also occur in New Guinea (Menzies & Dennis 1979). The grinding surfaces of the molars are basin shaped and lack cusps, possibly as an adaptation to a diet of aquatic invertebrates (Woollard, Vestjens & Maclean 1978).

Xeromys

(Weight about 40 g) False Water Rat

One rare species occurs which is distantly related to Water Rats, the other Australian member of the Hydromyini. The few specimens collected have come from the habitats bordering either salt or fresh water swamps and mangrove swamps (Magnusson *et al.* 1976). This species shows fewer adaptations to a semi-aquatic lifestyle than Water Rats, but it does have short, water-repellent fur, elongated nostrils and small eyes. Very little is known of its biology.

Mesembriomys

(Weight 200-900 g) Tree-rats

The two species, Black-footed and Golden-backed (*M. macrurus*) Tree-rats, are tree rats, but come down to the ground to forage. The former is a large animal that lives in tree holes in open forest and woodland habitats. The latter is smaller and lives in vine thickets and woodland. Both occur in the northern tropics and are rarely encountered. Little is known of their biology.

The Black-footed Tree-rat is unusual among murid rodents in having a long oestrous cycle (26 days) maintained by an active corpus luteum (Crichton 1969).

Conilurus

(Weight 150-200 g) Rabbit-rats

This genus of tree rats (two species only) is closely related to *Mesembriomys* and also inhabits open forest and woodland. One species, *Conilurus albipes*, occurred in south-eastern Australia, but is now extinct. The other, the Brush-tailed Rabbit-rat, is relatively common in restricted parts of coastal northern Australia. It also occurs in the open woodland of southern New Guinea (Menzies & Dennis 1979). There are two tail colour variants, one totally black and one with a white tip; both interbreed in the laboratory. Laboratory colonies are very successful and family groups are socially tolerant.

Zyzomys

(Weight 40-150 g) Rock-rats

Three species of *Zyzomys* inhabit rocky outcrops and scree slopes in tropical and central Australia. Aggressive towards each other, they hold territories around a rock face (Begg 1981c). Fat is stored in the tail in the same way as some of the small dasyurid marsupials. The tail skin is fragile and strips easily, possibly as a defence against predators.

Notomys

(Weight 25-60 g) Hopping-mice

Only five of the nine species of *Notomys* are extant. They are all small, bipedal, nocturnal animals of arid and semi-arid regions. Most species appear to live in burrow systems in sandy soil, some in colonies. The genus is basically granivorous, but some green vegetation and insects are eaten (Watts 1970). Individuals of some species can live without free water and can rear young under these conditions (Baverstock & Watts 1975).

The Spinifex Hopping Mouse is the best studied species. It has adapted to captive conditions and is used widely as a laboratory animal. As far as is known all species have a glandular area on the chest and throat in one or both sexes, the precise function of which is unknown (Bourne 1934; Watts 1975b).

An unusual feature of the reproduction is the small size of the internal male reproductive organs in several species. These are only about 1/10 the size found in most rodents of similar size (Breed 1981b).

Pseudomys

(Weight 8-90 g) Pseudo-mice

This large genus contains a heterogeneous assemblage of 22 species. Several subgenera have been used to divide the genus and it would not be surprising to have several separate genera erected in the future. Most live in arid, semi-arid or heathland conditions, but the Long-tailed Mouse and the Hastings River Mouse (*P. oralis*) live in dense forest. Some arid zone species survive without free water and produce urine among the most concentrated known in mammals (Baverstock & Watts 1974; MacMillen & Lee 1969). One species, the Delicate Mouse (*P. delicatulus*), occurs in the savanna woodland of southern New Guinea as well as northern Australia. The heterogeneity of *Pseudomys* makes it very difficult to make generalisations about the morphology or biology of the genus.

Mastacomys

(Weight 100-200 g) Broad-toothed Rat

The single species, *Mastacomys fuscus*, is closely related to *Pseudomys* species, but distinguished by greatly enlarged molars which are correlated with a diet predominantly of grasses and seeds (Watts 1977). It is known from alpine areas of south-eastern Australia and Tasmania and also widespread at low densities in lower altitude forests of Victoria (Seebeck 1981a).

Leporillus

(Weight 150-450 g) Stick-nest Rats

One of the two species in this genus, *Leporillus apicalis* is extinct. The other, the Greater Stick-nest Rat, is found today only on Franklin Island in South Australia where a population of 700 to 1000 still exists (Read 1984c). At the time of European settlement, both species occurred widely across the mallee and mulga regions of southern Australia where they built large nests of interwoven sticks around bushes, under rock overhangs and in the open. These were often massive structures measuring 2–3 m in diameter and 1–1.5 m in height. Each was occupied by a few individuals, probably family groups. The diet, from limited evidence, consisted predominantly of succulent vegetation (Watts & Eves 1976). Associated with many old nests in overhangs are solid masses of consolidated faeces and urine resembling the cave bitumen described from *Neotoma* nests in North America (Van Devender 1983).

Leggadina

(Weight 15-25 g) Short-tailed Mice

Two species, Forest's Mouse (*Leggadina forresti*) and the Lakeland Downs Mouse (*L. lakedownensis*), are found in grassy habitats in central and northern Australia. *Leggadina* is characterised by forward projecting upper incisors, which gives these species a buck-toothed appearance, and by the tail which is shorter than the head/body. Little is known of their biology either in the field or laboratory.

ACKNOWLEDGEMENTS

In addition to the obvious debt to many of our colleagues and predecessors we would like to acknowledge the help received from Dr R. Baudinette and Dr W. Breed in the preparation of this Chapter.

Mrs P.K. Kidd and Mrs D. Brunker variously typed the drafts of the Ms and prepared computer lists.

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