



FAUNA *of* AUSTRALIA

46. SCIURIDAE

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DEFINITION AND GENERAL DESCRIPTION

Squirrels, family Sciuridae are represented in Australia by two introduced species, the American Grey Squirrel (*Sciurus carolinensis*) Gmelin 1788 and the Northern Palm Squirrel (*Funambulus pennantii*) Wroughton 1905.

Sciurids are distinguished from the only other family of Rodentia in Australia, the Muridae, by their external form, in particular a tail bushy to the base, and by skull differences, notably the presence of premolar teeth and a pronounced supra-orbital spine (Watts & Aslin 1981).

HISTORY OF DISCOVERY

Both species were privately introduced to Australia in the 19th Century; Grey Squirrels to Melbourne, Victoria, about 1880 (Seebeck 1984) and Palm Squirrels to Perth, Western Australia about 1898 (Jenkins 1977). Subsequently, Grey Squirrels were introduced to Ballarat, Victoria, in 1937 and Palm Squirrels to Taronga Zoo, Sydney, New South Wales, perhaps during the 1920s.

The Grey Squirrel is now apparently extinct in Australia (Seebeck 1984). Palm Squirrels are extinct in Sydney, but a flourishing feral colony based on Perth Zoo still exists. A captive colony has been established (1979) at Melbourne Zoo, Victoria. A similar colony at Adelaide Zoo has died out.

Museum specimens of Grey Squirrels (from Ballarat) are housed at the Museum of Victoria (Seebeck 1984), and of Palm Squirrels at the Western Australian Museum, the Australian Museum, the South Australian Museum and the Australian National Wildlife Collection (CSIRO).

Research on both species in Australia has mostly been limited to recording distribution and anecdotal information on habits and behaviour (Barrett 1934; Sedgwick 1968; Watts & Aslin 1981; Seebeck 1984), although one post-graduate study was carried out on Palm Squirrels (Wright 1972). Both species have been studied extensively overseas: Grey Squirrels in the United States and England (Shorten 1951; Lloyd 1962; Madson 1964; Barkalow & Shorten 1973) and Palm Squirrels in India and Pakistan (Prasad *et al.* 1966; Purohit, Kametkar & Prakash 1966; Prakash, Kametkar & Purohit 1968; Prakash 1975; Chaudry & Beg 1977).

Australian zoos, at times, have exhibited perhaps a dozen other species of sciurid, including species of *Sciurus*, *Callosciurus*, *Ratufa*, *Cynomys* and *Marmota* (Rix 1978), but none of these has ever established feral populations.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics, Size and Body Wall

Both species are characteristically squirrel-like in appearance, with close, dense body fur and thick bushy tails, which Grey Squirrels can hold up and forward along the back. They have a broad, rounded head with large eyes and prominent rounded or triangular ears (Fig. 46.1).

The Grey Squirrel is dorsally a grizzled pale grey, due to the long straight guard hairs which are banded alternately grey and white. A rufous colouration suffuses the head, ears and in the axils of the forearm. There is a faint rufous mid-dorsal stripe. The belly is white, as are the feet. The tail fur is very long (at least four



Figure 46.1 Northern Palm Squirrels shown foraging. (© ABRS) [K. Hollis]

times the length of the body fur), banded alternately dark grey and white, and intermingled with some rufous hairs, giving a grizzled appearance that is darker than the body. When flattened the tail appears to be edged with white.

The Palm Squirrel is light brown on the head, ears and feet and has deep red-brown dorsal fur. It is marked antero-posteriorly by five pale stripes, three of which extend from the neck to the base of the tail. The outer two stripes extend only from the fore- to the hind leg. The belly is white. The long tail hair is banded alternately dark brown and white-pale brown, giving a grizzled appearance.

In its Northern Hemisphere environment, Grey Squirrels weigh 400–500 g (although specimens up to 800 g have been reported), have a total length of about 460 mm including a tail of about 215 mm (Barkalow & Shorten 1973; Tittensor 1977). Victorian specimens from the Ballarat colony were generally close to these dimensions (Seebeck 1984).

Palm Squirrels are much smaller. Adults weigh about 135 g, but may reach nearly 200 g (Wright 1972). Watts & Aslin (1981) quote size as total length 250–270 mm and tail length 110–120 mm. Nine live animals measured by Scanlan, Gorton & Pearsall (1978) averaged 243 mm (range 200–300 mm) and a specimen in the Western Australian Museum has a total length of 292 mm.

Skeletal System

Both species have conventional small mammal skeletal systems, although the ankles, as in all tree-squirrels, display extraordinary rotational capabilities, an adaptation for arboreality. Dentition in the sciurids (Fig. 46.2) differs from that of Australian native and introduced rodents (Family Muridae) by the presence of premolars, which are simple or molariform. The skulls are distinguished from those of murids by the presence of a pronounced supra-orbital spine and a small infraorbital foramen which is rounded, never slit-like. The tibia and fibula are separate. Sharp, curved, non-retractable claws aid in climbing.

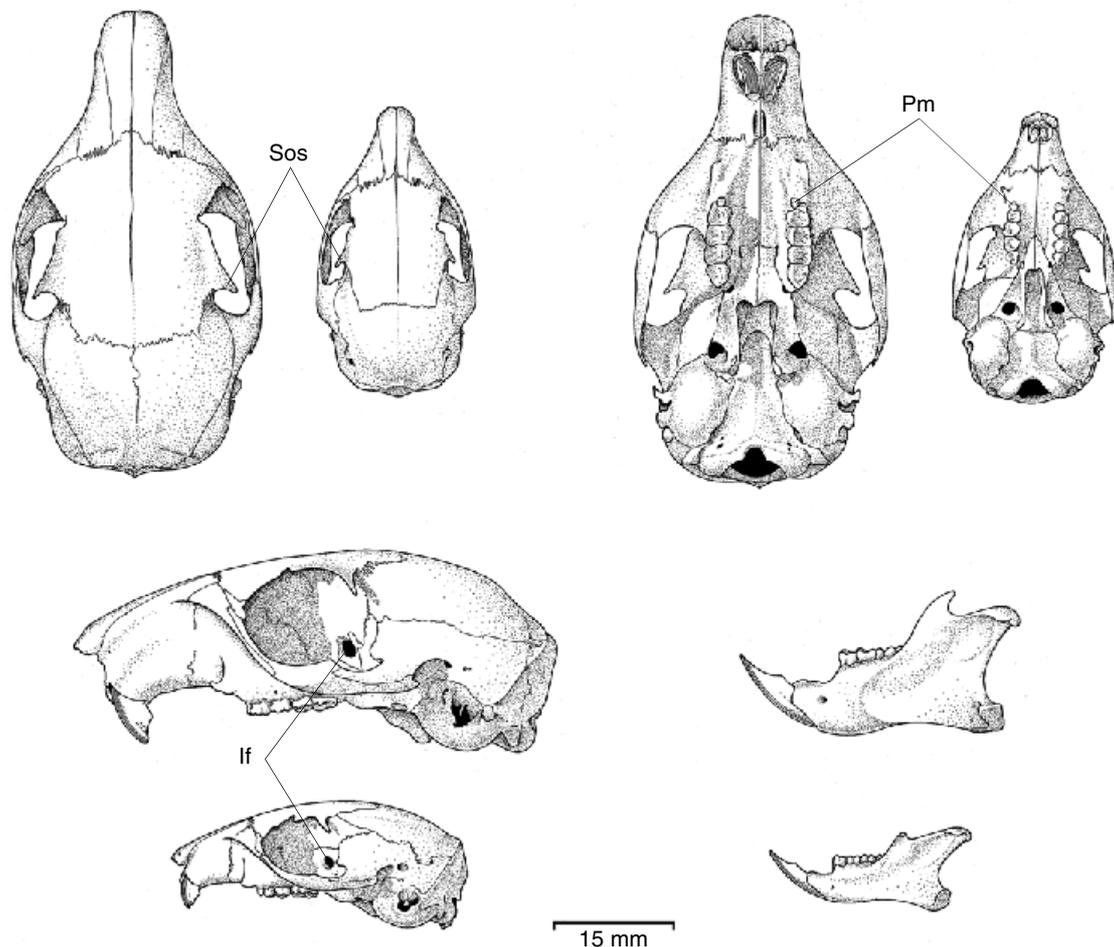


Figure 46.2 The skull (A-F), in dorsal, lateral and ventral view, and lateral view of the mandible (G, H) of squirrels. A, C, E, G, the American Grey Squirrel, *Sciurus carolinensis*, and the Northern Palm Squirrel, *Funambulus pennanti*. (© ABRS) [G. Milledge]

Locomotion

Both squirrels are highly mobile, agile climbers, with the ability to jump rapidly and surely within the tree canopy or onto the ground. Grey Squirrels can run rapidly and speeds of up to 28 km / hour across open ground have been recorded (Layne & Benton 1954). They are also accomplished swimmers (Barkalow & Shorten 1973).

Feeding and Digestive System

Both species are essentially herbivores, but their diet includes some animal material. In its native North American forests and in Great Britain, the Grey Squirrel feeds predominantly on acorns and nuts, particularly hickory nuts, as well as pecan, walnut, hazel and beech, among others. In spring, buds and flowers, especially pollen-rich male flowers of hardwoods, are eaten. Berries, fungi and bark are included in the diet and browse may be taken when food is scarce (Barkalow & Shorten 1973). In Great Britain, apparently in the search for sweet sap (Kenward 1984), these squirrels strip the bark of trees, particularly in plantations of beech and sycamore, and can cause considerable damage. Their numbers are controlled by shooting or poisoning.

Insect larvae and pupae are eaten when available, but not in large quantities. Madson (1964) reported that as much as 4% of their diet may consist of such material. Squirrels sometimes take eggs, nestlings, frogs and lizards and may obtain minerals and some vitamins by eating soil. Because Vitamin D forms on the fur in sunlight they ingest it during grooming (Barkalow & Shorten 1973). In Melbourne and Ballarat Grey Squirrels were fed cereals, especially maize, but obtained nuts, acorns, soft fruits (especially Moreton Bay Fig), seeds and berries as well as kitchen refuse from suburban parks and gardens. They drink water although some is obtained from their food.

The Grey Squirrel feeds in the tree canopy, frequently hanging head-down amongst the branches and holding food with its forepaws. When feeding at ground level, it may use a stump or log as a feeding table. Animals of this species eat about 90 g (fresh weight) of food per day (Madson 1964) and coprophagy has been observed. A digestive tract about 2.2 m long (Barkalow & Shorten 1973) and a relatively large caecum (90 mm), are well suited to this process (Barkalow & Shorten 1973).

As Grey Squirrels cannot hibernate they store food for the severe Northern Hemisphere winter by burying single nuts or acorns in the soil, from which they are retrieved when needed. The species is very efficient at finding buried food by scent. At Ballarat, Grey Squirrels regularly cached food (the process is instinctive), but population numbers were never sufficient for all such caches to be relocated.

Palm Squirrels eat seeds throughout the year, leaves and soft fruits during autumn, and insects, particularly locusts, during summer and do not cache food. Near human settlements, they feed extensively on kitchen refuse. In Perth, Sedgwick (1968) reported that they fed on refuse and food scraps (especially bread). Wright (1972) observed them in the Perth Zoo grounds feeding on the following: fruits of *Phoenix*, *Ficus*, *Morus* and *Melia*; seeds of *Brachychiton*; cones of *Araucaria* and *Pinus*; buds, grass, insects and animal food. Scanlan *et al.* (1978) reported that Palm Squirrels eat fruit, leaves and food scraps.

The dental formula for both species is I 1/1 C 0/0 PM 2/1 M 3/3. The incisors grow continuously and are maintained chisel-sharp, whereas the molars are rooted and have prominent ridges and cusps. PM1 is a simple, peg-like tooth, but PM2 is molariform.

Circulatory and Respiratory Systems

Both species of squirrel have systems typical of small mammals and are not reported to have any particular specialisation. Although it cannot hibernate, the Grey Squirrel may reduce its activity during short periods of adverse weather during the Northern Hemisphere winter.

Excretion

Excretory systems in both species are typical of small mammals. Grey Squirrels produce a few faecal pellets at a time and drops them haphazardly within their home range. The animals do not foul their nest with droppings which are typically tapered cylinders with a conical projection at one end and measure about 10 x 6 mm. The colour of the faeces depends on diet.

The Grey Squirrel partially marks territory with urine containing secretions from Cowper's glands (Barkalow & Shorten 1973).

Sense Organs and Nervous System

Grey Squirrels have large, mobile nostrils, large nasal cavities and appear to have a well-developed olfactory system, which they use to locate food and to follow scent trails during breeding or range-patrolling. Large ears aid in the reception of community auditory signals. Vibrissae are well developed around the head, especially the mouth, and also on wrists, anus and nipples. Large, dark eyes on the sides of the head give a very large field of vision. Stereoscopic vision is well developed, as is upward vision as a protection from aerial predators. The retina has cones only and visual acuity is, therefore, outstanding. The species has poor visual sensitivity, as is typical of a diurnal organism and is most active when light intensities are moderate. The eye has no tapetum and, hence, no eyeshine. The presence of cones only in the retina and the striking colours and coat patterns of both Palm and Grey Squirrels suggest that colour vision is well developed, but the Grey Squirrel is not thought to have regular trichromatic vision (Barkalow & Shorten 1973).

Endocrine and Exocrine Systems

The endocrine glands of both species seem characteristic of small mammals. Prasad *et al.* (1966) have described changes in the cytology of the pituitary gland of Palm Squirrels and observed that adrenalectomy of females resulted in the development of adrenal-like tissue in the ovary.

The squirrels' exocrine glands are characteristic of the small-mammal type. The Grey Squirrel has four pairs of functional mammae serving the mammary glands, Palm Squirrels have but two pairs. Differences in the male reproductive glands are recognised. Grey Squirrels have large, well-developed Cowper's glands which secrete wax that 'fixes' reproductive odours in urine, whereas Palm Squirrels have minute Cowper's glands. In both species, the weights of testis and accessory gland show cyclic changes. Both species also have sweat glands on palms and soles and also may have apocrine glands in the mouth to mark food or food sites. The sweat glands possibly are used in range marking.

Reproduction

The male reproductive tract of the Palm Squirrel has been described as a non-penile duct type, but the Grey Squirrel, like most squirrels, has a penile duct type tract and thus is quite different (Prasad *et al.* 1966). Female reproductive tracts in both species are typical of rodents.

Courtship and mating of Palm Squirrels involves chasing and tail-biting a single female by several males, together with male-male fighting. A female waits, calling, until the victorious male chases her before overpowering, mounting and mating; this occupies 10–20 minutes. Females are submissive during mating although twining of tails may occur and biting by the female may end matings. Females will mate three to four times during the day with the same or different males. Breeding is seasonal in India from February to September with peaks in April and September. Males are reproductively quiescent between November and January. Gestation lasts about 42 days, and one to five young, usually two to three, are born in a grass and fibre nest usually placed in a tree, wall or roof. Weaning takes place at about 10 weeks and sexual maturity is reached at 8–9 months. Mature females may have two litters per year. Sex ratio at birth is about 1:1, but in India female mortality is higher and the adult sex ratio is 2.3:1 (Purohit *et al.* 1966; Prasad *et al.* 1966; Chaudry & Beg 1977). In Australia, the species breeds between August and May, with peaks in October and April. The recorded sex ratio for Palm Squirrels at Perth Zoo was 1:1 except during May, when no adult males were trapped. Litter size averaged 2.5. Nests (of palm fibre, jute sacking, grass or wool) were placed in Phoenix, Melia, Agonis, Pandanus trees or in clumps of bamboo (Wright 1972).

Grey Squirrel courtship and mating is also polygamous and involves chasing and display. Breeding is seasonal, the species breeding in North America during spring and summer. Males are reproductively quiescent in autumn, but may be fecund all year in England. Females are polyoestrus, display no post-partum oestrus and are anoestrus between September and December. The length of the breeding season depends on food availability and climatic conditions. In Australia, breeding was reported during late spring-late summer (October to February). Gestation lasts 42–45 days and one to nine young, usually three to four, are born in an untidy twig and leaf nest (drey) lined with soft fibre and usually built in a tree fork. If disturbed, females may transport young by carrying them in the mouth. Weaning occurs between 7 and 10 weeks and sexual maturity is usually at 10–12 months, although precocious breeding has been reported (one female in the United States gave birth at 168 days – less than 6 months old). Mature females in the Northern Hemisphere may have two litters per year, yearlings only one. Sex ratio of nestlings was 1.1:1, but for adults it was 0.85:1 (Barkalow & Shorten 1973). Two to three litters per year were reported for the Australian population (Watts & Aslin 1981).

Embryology and Development

Newborn Palm Squirrels are naked and pink, although incipient dorsal markings are visible. Vibrissae are present, eyes are closed and the pinnae are folded. Measurements are about 50 mm head & body, tail about 30 mm, pes about 12.5 mm and weight 5–8 grams. Young vocalise within a week of birth and are capable of uncoordinated movement. Their eyes open at 15–25 days and pinnae unfurl at 7–10 days. The pelage develops uniformly, with dorsal stripes becoming prominent in the second week and mature colouration attained in 8–10 weeks. Teeth are not visible in newborn young, but lower incisors may be visible in young a week old. Upper incisors usually erupt later and adult dentition is complete at 12–13 weeks. More than 70% of growth of young occurs in the first 8 weeks after birth. A hand-reared litter in Perth (Scanlan *et al.* 1978) appeared to follow the general growth trends described by Purohit *et al.* (1966), but Wright (1972) found that wild-caught young in Australia at 4–5 weeks old were almost twice the weight reported by Purohit *et al.* (1966) for Indian animals.

Grey Squirrels are also born naked and pink, with vibrissae visible, eyes closed and ears furred. Total length is about 115 mm and weight 13–17 grams. They can vocalise within hours of birth. Their eyes open at about 28–35 days and

pinnae unfurl at about 1 week, but ear canals remain closed until 25–28 days. Pelage develops uniformly from about 2 weeks and the nestling coat is replaced by seasonal coat at 13–16 weeks. Lower incisors erupt at 21 days, upper incisors at 28–35 days and molars about 6–7 weeks. Full growth is reached at about 6 months (Barkalow & Shorten 1973; Tittensor 1977).

NATURAL HISTORY

Life History

Both species may become reproductively mature at about the same age (see above) and both produce about the same number of young per year. Older females produce more litters annually than do yearlings, but generally, fecundity depends on the availability of food and comfortable climatic conditions during the breeding season.

Mortality among juvenile Palm Squirrels in Perth was about 30% (Wright 1972). The species is not long-lived, Chaudry & Beg (1977) reported longevity of up to 18 months in the wild in India, but suggested it could be longer. No information on the Australian population is available.

Grey Squirrels have been kept captive for up to 20 years, but survival in the wild being low (less than 25%) during the first year, their life expectancy is only about 1 year. If young animals survive beyond this, they frequently live much longer, most as long as 7–8 years, a survival rate of greater than 52%. Barkalow, Hamilton & Soots (1970) derived a longevity of 9 years for free-living individuals. A captive Grey Squirrel at Ballarat (Victoria) lived for longer than 13 years (Seebeck 1984). Adult females have a slightly higher survival rate than adult males. Barkalow *et al.* (1970) calculated that cohort longevity was 6.4 years based on a 99.5% turnover in the population. No information is available for the Australian population.

Ecology

In India and Pakistan, the Palm Squirrel is a common and widespread commensal, found in homes, gardens and roadside trees. It is completely diurnal and generally arboreal. In particularly arid parts of its range, thick foliage and the moist microclimate of trees, particularly in orchards, provide shelter from excessive climatic conditions (Ghosh 1975). Prakash (1975) found it to be uncommon in the desert biome of north-west India where it was found most frequently in rocky and ruderal areas.

It has not adapted to natural environments in Australia, and is restricted to suburban and/or plantation areas close to the original release sites. In Perth, the population still occupies an area of only about 30 km²; in Sydney the area occupied was smaller. Palm Squirrels shelter in introduced trees or buildings and the population is limited by 'natural' food availability. At Como High School, Perth, the population decreased during school vacations when additional food was unavailable (Scanlan *et al.* 1978). Wright (1972) found that the population density was greatest in areas of Perth Zoo that had the highest density of fruiting and nest trees, and that were closest to a supply of supplementary food. From this, she inferred that these were major limiting factors in the spread of the species in Perth. The Perth Zoo population was estimated to consist of about 1000 animals (Wright 1972).

Prakash *et al.* (1968) found that in India home ranges were overlapping for both sexes – about 0.2 ha for males, and about 0.15 ha for females. Wright (1972) determined the home ranges (both sexes combined) in Perth Zoo of between 0.02 and 0.26 ha. Observed range length in India was 60–70 m for males,

40-50 m for females; in Perth the range was 50–135 m, that of males averaging about 90 metres. The species is not territorial, although the animals may defend nest and roost sites. Dominant males, may however, kill persistent intruders. During reproductive activity, females are thought to initiate courtship.

Predation in the wild is apparently low (varanid lizards are reported predators). In Australia, introduced mammalian predators do not seem to be a major problem, but corvids and diurnal raptors harass squirrels (Scanlan *et al.* 1978). Wright (1972) reported predation of Palm Squirrels by captive hawks and broilgas at the Zoo and by rats, cats and Nankeen Night-herons. Perhaps the greatest predation was by humans; active population culling by Zoo staff is used to limit populations and there may be some mortality during and consequent upon annual pruning of palm trees. Road casualties are another human-based cause of mortality.

No specific diseases have been reported for the species. In India, several nematode parasites have been reported (Johnson 1975) and in Australia, megostigmatid mites (*Ornithonyssus bacoti*) were present on some squirrels (Agriculture Protection Board of Western Australia, personal communication 1986). Wright (1972) found a coccidiosis, possibly *Eimeria sciuri*, in the gut of two specimens examined.

The native habitat of the Grey Squirrel is dense hardwood forests, particularly those of oak, hickory and walnut, but in Australia it was found only in suburban parks and gardens (Seebeck 1984). It never became established in natural forest and healthy populations seemed to depend on being fed by humans. In North America, the species encounters some competition from the Fox Squirrel (*Sciurus niger*) and in the United Kingdom, the Grey Squirrel has been implicated with a dramatic reduction in range of the European Red Squirrel (*Sciurus vulgaris*). Recent work suggests that it is effective in preventing recolonisation by the latter species (Tittensor 1977).

The flea *Orchopeas howardi*, is specific to the Grey Squirrel with which it was introduced to England, but is not recorded from Australia, although other fleas, mites and lice have been reported. Viruses (foot and mouth disease, leptospirosis, mange), coccidiosis and shock disease are reported for Grey Squirrels (Tittensor 1977).

Predation in the wild, especially on young animals, is widespread and many natural predators are implicated. In Australia, dogs, cats and humans were important predators (Seebeck 1984). Reported overlapping home ranges varied from 1–20 ha, with male ranges greater than those of females. Population densities range between one and 13 squirrels ha⁻¹ and often depend on food abundance. At Ballarat, the maximum population was estimated as about 100, a density of about 1 ha⁻¹. Mass migrations have been recorded in North America, but not in other populations – these are thought to be the result of food crop failure.

Behaviour

Feeding behaviour, courtship and reproductive behaviour are described above. Feeding and other activities are generally not observed until several hours after sunrise and there is a peak in activity 1–2 hours before sunset (Wright 1972). Basking is a usual precursor to morning activity and as shade increased in late afternoon, the animals tend to be quiet. Palm Squirrels avoid heat stress by sheltering in canopy vegetation and limit foraging activity when ambient temperatures are high (Ghosh 1975). Squirrels are tolerant of each other when feeding, often forming large groups. Scanlan *et al.* (1978) observed much chasing upon encounter, accompanied by chattering. Squirrels at Como High School, Perth, tended to seek shelter when students were out of class and be active in the open during class hours.

Grey Squirrels operate to a different time schedule. They are most active at first light and at the end of the day. Most of their day is spent either in the nest or roosting, often basking in full sun. Activity may continue throughout overcast days or even on bright moonlit nights (Madson 1964). Play activities—running, jumping, chasing—were all reported in Australian colonies by Seebeck (1984).

Economic Significance

Neither species has economic significance in Australia, except by causing minor damage to garden plants and as a tourist attraction (Palm Squirrels in Perth Zoo, formerly at Taronga Zoo, Grey Squirrels formerly at Ballarat Gardens). The Palm Squirrel is considered a potential pest species in Western Australia and has been a Declared Animal (Vermin) in that State since 1973 (Agriculture Protection Board of Western Australia 1985). A few of these animals, inadvertently translocated, have been found (and destroyed) in remote areas as far as 140 km from Perth. It is a common commensal in northern India, but does not seem to be a major problem. In the United States, the Grey Squirrel is the third most important game animal, with millions being taken annually for meat and pelts. In the United Kingdom, it is declared vermin because of its damage to forests (particularly hardwood plantations) and its presumed replacement of the indigenous Red Squirrel (Madson 1964; Barkalow & Shorten 1973).

There is a potential pet trade in Palm Squirrels and because of the zoo population in Melbourne, there is a possibility a feral population might be established there.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Distribution of both species in Australia is described above. Grey Squirrels are native to the eastern United States and south-eastern Canada and have been introduced to western United States and to other provinces in south-eastern Canada. They have also been introduced into England, Scotland, Wales, Ireland and South Africa. The Palm Squirrel occurs naturally in northern India and in Pakistan.

Affinities

Ellerman (1940) included both species in the Group Sciuri (the non-volant forms) within the Family Sciuridae. He considered the genera *Funambulus* and *Sciurus* to be related closely and had difficulty in defining them as separate genera, although ultimately he retains *Funambulus* as a 'natural group'.

COLLECTION AND PRESERVATION

In Australia, both species have been collected by live-trapping in baited cage traps, although the Palm Squirrel seems to be easier to capture than the Grey (Seebeck 1984). Wright (1972) used a multiple-capture drum trap with a funnel entrance, baited with bread and apples to trap Palm Squirrels, and in three short (3–4 days) trapping sessions with 30 such traps, caught more than 270 animals. Other specimens were shot. The feral population at Taronga Zoo was reduced to extinction largely by rat poison. Existing museum specimens are retained as puppet skins and skulls, but future specimens should be maintained in the Western Australian Museum as wet specimens.

Identification

Members of the Sciuridae are distinguishable from the Muridae by a tail that is bushy to its base, the presence of a supra-orbital spine, premolars and the shape of the infraorbital foramen.

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