



# FAUNA *of* AUSTRALIA

## 28. FAMILY PETAURIDAE

G.M. McKAY



Mahogany Glider—*Petaurus gracilis* [Queensland Museum]



Sugar Glider—*Petaurus breviceps* [CSIRO Wildlife & Ecology]



Greater Glider—*Petauroides volans* [CSIRO Wildlife & Ecology]



## DEFINITION AND GENERAL DESCRIPTION

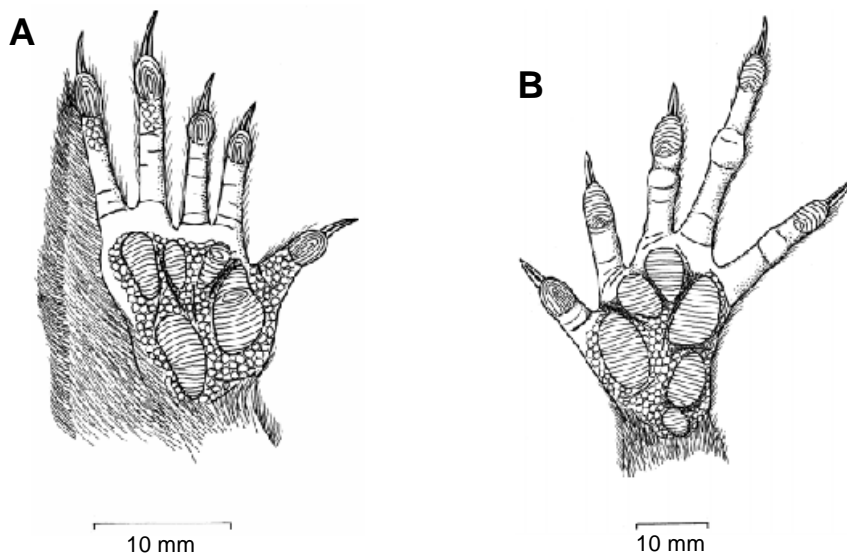
The family Petauridae contains 23 species, 11 of which occur in Australia. The family was subdivided into three subfamilies by Kirsch (1977a): Petaurinae, Pseudocheirinae and Dactylopsilinae. As discussed below, the family as currently constituted may represent an artificial grouping of at least two families. Petaurids are small mammals ranging from 150–450 mm head and body length and 100–2000 g in weight. All species show a general arboreal adaptation, including feet adapted for grasping and a long prehensile or semi-prehensile tail.

Petaurids are diprotodont with a dominant pair of large lower first incisors. On the hind foot the hallux is opposable and clawless and the second and third digits are syndactylous as in the other phalangeroid families. The pouch opens anteriorly and contains either two or four teats. The pouch is frequently divided into two incompletely separated compartments by a median septum. In the digestive tract, the caecum is very small in the subfamily Dactylopsilinae, large in the Petaurinae and greatly enlarged in the Pseudocheirinae in which it acts as a fermentation chamber.

No single character uniquely defines the Petauridae, but several characters distinguish the three subfamilies from all other phalangeroids.

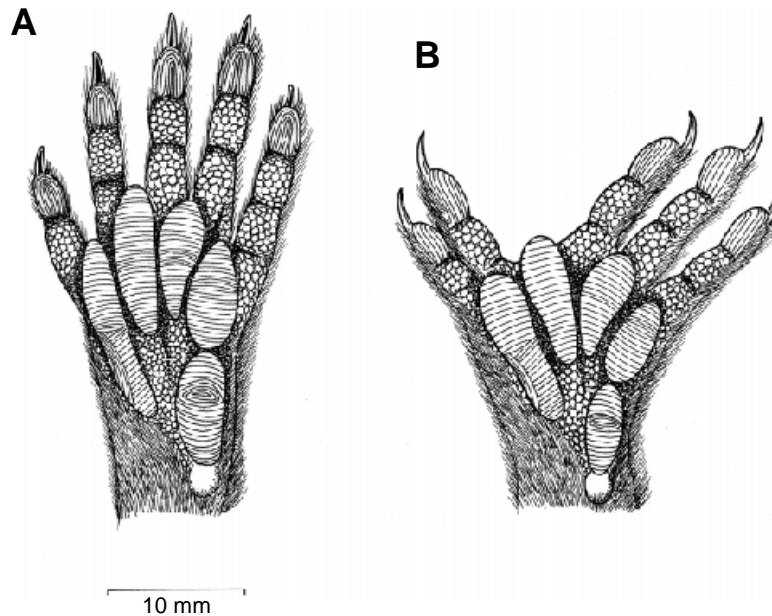
In the Petaurinae, the manus shows no specialisation for climbing other than enlarged claws. The tail is semi-prehensile and entirely furred. In *Petaurus* species, a patagium or gliding membrane extends from the base of the fifth manal digit to the metatarsal region. Pelage colour is variable, but there is generally a prominent dark mid dorsal stripe.

The manus of the Dactylopsilinae shows a remarkable adaptation paralleled only by the primate, *Daubentonia madagascariensis*, of Madagascar. The fourth digit is considerably elongated as an adaptation for feeding. compares The manus of the Striped Possum, *Dactylopsila trivirgata*, is compared to that of *Petaurus* species (Figure 28.1). The prehensile tail is fully furred except for a small ventral naked patch at the tip. Pelage colour is a striking contrast of black and white antero-posterior stripes.



**Figure 28.1** Comparison of the left manus of: **A**, *Petaurus*; **B**, *Dactylopsila* showing the markedly elongated fourth digit in the latter. (After Dixon & Huxley 1985; © ABRS) [S. Weidland]

In the Pseudocheirinae, the first two digits of the manus (Fig. 28.2) are at least partly opposable to the remaining three as an adaptation for grasping small branches. The prehensile tail may have a ventral friction pad of naked calloused skin or only a small naked area at the tip (Fig. 28.3). The Greater Glider, *Petauroides volans*, has a patagium extending from the elbow to the lower portion of the tibia. Pelage colour is highly variable between species of this subfamily and, occasionally, within a species.



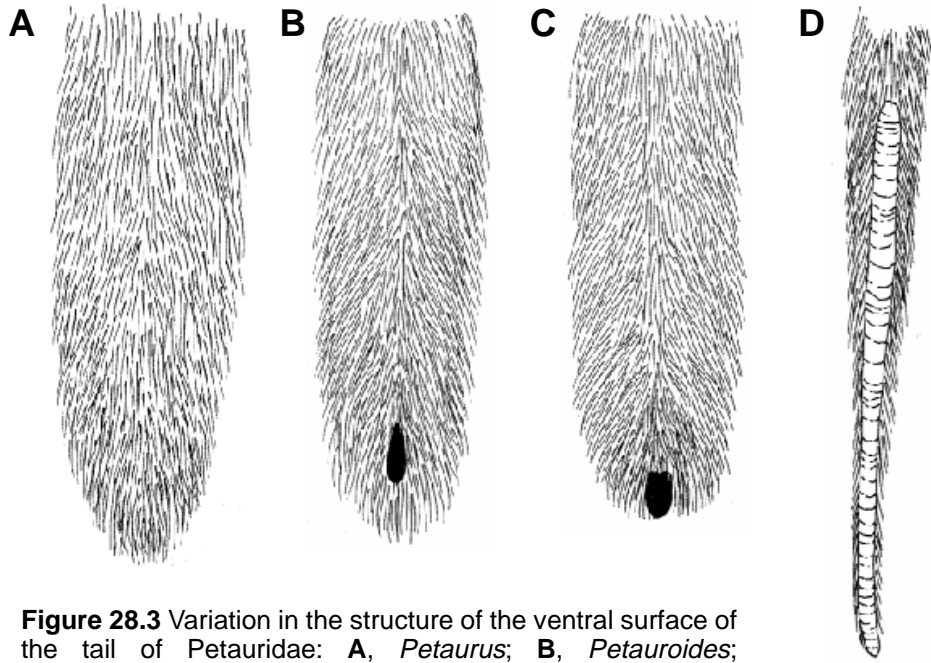
**Figure 28.2** Left manus of *Pseudocheirus* showing: **A**, the digits closed; **B**, digits open in position for grasping. (After Jones 1924; © ABRs)

[S. Weidland]

Three pairs of upper incisors are present. The first pair is normally longer than the succeeding pairs and projects anteriorly in the Petaurinae and Dactylopsilinae. The upper canines are generally as small as the final incisors, but may be larger and laterally compressed in the Petaurinae. Three upper premolars are always present and the first two pairs vary in shape and size. The third pair is larger than the second and is elongated with two or three cusps in the Pseudocheirinae, but conical with a single cusp in the other subfamilies. Four pairs of upper molars are present in the adult, with the fourth smaller than the preceding three. In the Pseudocheirinae, these molars are strongly selenodont, with crescent-shaped ridges connecting the cusps. In the other two subfamilies they are bunodont, with four low pointed cusps.

On the lower jaw, the procumbent first incisors are compressed and blade-like in the Pseudocheirinae, slightly curved in the Petaurinae and strongly curved and greatly enlarged in the Dactylopsilinae. A second pair of vestigial incisors is present in most species, but these may be lost in some Pseudocheirinae. Three pairs of small premolars are present in the Petaurinae and Dactylopsilinae. In the Pseudocheirinae, the third lower premolars are large, only slightly smaller than the first adult molars. The first and second premolars may be either vestigial or absent. In the Petaurinae and Dactylopsilinae, the lower molars decrease in size from first to fourth, but in the Pseudocheirinae all are approximately equal in size. Crown adaptations of the lower molars are similar to the upper molars.

In dorsal aspect, the rostrum or snout region of the skull is markedly pointed and the zygomatic arch is slender and rounded in all but the Pseudocheirinae, where it is more robust but not so wide. There is a tendency in all groups for swelling



**Figure 28.3** Variation in the structure of the ventral surface of the tail of Petauridae: **A**, *Petaurus*; **B**, *Petauroides*; **C**, *Hemibelideus*; **D**, *Pseudocheirus*. (© ABRS) [S. Weidland]

of the squamosal bone at the posterior margin of the zygomatic arch. Posterior palatal vacuities may be present in the Pseudocheirinae, but are absent in the other two subfamilies.

Diagnostic characters for each subfamily are as follows: Petaurinae: three single cusped upper premolars, the first and second laterally compressed; molars bunodont, decreasing in size from first to last; palate without posterior vacuities; second to fifth manal digits all subequal in length. Dactylopsilinae: three single cusped upper premolars, the second considerably smaller than the first; molars bunodont, decreasing in size from first to last; palate without posterior vacuities; fourth manal digit distinctly longer than the fifth. Pseudocheirinae: three upper premolars, the third bearing two or three cusps; molars selenodont; the first two manal digits at least partly opposable to the others.

## HISTORY OF DISCOVERY

The first petaurid to be discovered by Europeans was a Common Ringtail Possum, *Pseudocheirus peregrinus*, collected on Cook's first voyage in 1770. Unlike the first kangaroo, this specimen was not eaten by the crew of the *Endeavour*, but travelled safely to England where it was described accurately and figured by Pennant (1783) and later named *Didelphis peregrinus* by Boddaert (1785). The current generic name, *Pseudocheirus*, was established by Ogilby (1837). Pennant (1783) said this specimen came from the Endeavour River and in his journal Banks records finding 'an animal of the Opossum tribe' there (Beaglehole 1962). The colour of the animal described by Pennant (1783), however, does not match that of more recent specimens from north Queensland. Rather, his account gives an accurate description of the colour of specimens from around Sydney, New South Wales. A specimen of the Common Ringtail Possum in the Rijksmuseum van Natuurlijke Historie in Leiden, said by Temminck to be a Cook specimen (Jentink 1884) and matching Pennant's description (including the damage to the skull), is almost certainly from the Sydney area. Subsequent collections failed to find any Common Ringtail Possums closer than 200 km to Cooktown. The only large phalanger in the immediate vicinity of the Endeavour River is the Common Brushtail Possum,

*Trichosurus vulpecula*. Since the Leiden specimen cannot be stated unequivocally to be that collected by Banks, the exact type locality of this first important discovery must remain a mystery.

Cook's third voyage (1776-1780) produced a second specimen of a Common Ringtail Possum from Adventure Bay, Tasmania. This specimen is figured in the first account of the voyage (Cook 1784) with a description evidently copied from the journal of Anderson (Beaglehole 1967), but does not appear to have been preserved. The naturalists of the first fleet in 1788 produced the next series of specimens of Petauridae: three species of the highly specialised gliding forms. These are described, but not named, in two of the hastily published contemporaneous accounts of the new colony. The descriptions in these two works (Phillip 1789; White 1790) were used subsequently by Shaw (1791) in naming the Yellow-bellied Glider, *Petaurus australis* and by Kerr (1792) for the Squirrel Glider, *P. norfolcensis* (as *Sciurus*), and the Greater Glider, *Petauroides volans* (as *Didelphis*). The specific name *norfolcensis* arose from the erroneous opinion of the anonymous author of Phillip (1789), that the specimen came from Norfolk Island. Presumably, this was because it was obtained from a member of the crew of the *Supply* after its return from that colony. The general resemblance of the former two species to Northern Hemisphere squirrels, which are rodents, was to cause some initial confusion, as evidenced by Kerr's generic placement of *norfolcensis*. Indeed, Shaw, in his description of the Yellow-bellied Glider, states that he considered *Petaurus* to be a subdivision of *Sciurus*. These errors were corrected as more specimens became available. Shaw subsequently renamed the species as *Didelphis petaurus* and *D. sciureus* (Shaw 1800). Such early confusion did not attend the Greater Glider, which was immediately recognised as a marsupial. The type specimens of these three species appear to have been lost. These species still occur in the vicinity of Sydney, but the two most abundant species in the area today (the Sugar Glider, *Petaurus breviceps*, and the Common Ringtail Possum) apparently were not found by the naturalists of the First Fleet.

The next discovery in the Petauridae is significant mainly for the confusion it caused in the mid-19th Century. Péron and Lesueur, on their voyage with Baudin early in that century, collected primarily on Kangaroo Island and in Tasmania. Most of the descriptions of their specimens refer to animals from those two localities. While the naturalists were waiting in Sydney for the captain to purchase an extra ship for their further exploration, they spent at least some of their time collecting. Cayley (1966) reports that Lesueur obtained more than 200 specimens of birds and mammals. Among these were two *Pseudocheirus* species, one of which is still in the Muséum National d'Histoire Naturelle in Paris. In describing the specimens, Desmarest (1818) refers to Cook's similar specimen from Tasmania and appears to have considered them one and the same species. Subsequent workers, with the notable exception of Ogilby, assumed that the Lesueur specimens came from Tasmania and used *P. cookii* (Desmarest 1818) as the name for Tasmanian animals. The confusion was partly to blame for a sometimes acrimonious exchange of spoken and written words between Ogilby (of the Zoological Society) and his contemporary, Gray (of the British Museum) which can be read in the Society's proceedings. But, Lesueur's label on the specimen reads 'Australie' not 'Terre de Van Diemen'. The skull of the specimen is not of the robust Tasmanian morphology and Péron's illustration of the animal, a fine print of which hangs in Old Government House at Parramatta, is clearly of a Sydney animal.

There was then a gap of more than 30 years until the next Australian species, the Sugar Glider, *Petaurus breviceps*, was described by Waterhouse (1839). The next species to be recognised was Leadbeater's Possum, *Gymnobelideus leadbeateri*, from central Victoria (M'Coy 1867). M'Coy records two specimens; only three more were collected between then and 1909. It was presumed to be



extinct until rediscovered in 1961 (Wilkinson 1961). The Striped Possum, *Dactylopsila trivirgata*, was first discovered by Alfred Russell Wallace on the Aru Islands, west of Irian Jaya, in 1857 and subsequently was found by C. Coxen on Cape York in 1865. The Cape York specimen was described as a separate species by Thomas (1908).

During the mid-19th Century, several new forms which are now regarded as synonyms or subspecies of previously established species, were collected and described by several different authors. Carl Lumholtz, who collected a large series of animals in north Queensland, provided the specimens that were described by Collett (1884) as *Phalangista archeri* (Green Ringtail Possum) [now *Pseudochirops archeri* (ed.)], *Phalangista herbertensis* (Herbert River Ringtail Possum), and *Phalangista (Hemibelideus) lemuroides* (Lemuroid Ringtail Possum). All three were later placed in *Pseudocheirus*. *Pseudochirops dahli* (Rock Ringtail Possum) [now *Petropseudes dahli* (ed.)] was described by Collett (1895) from specimens collected by Knut Dahl in the Northern Territory.

## MORPHOLOGY AND PHYSIOLOGY

### External Characteristics

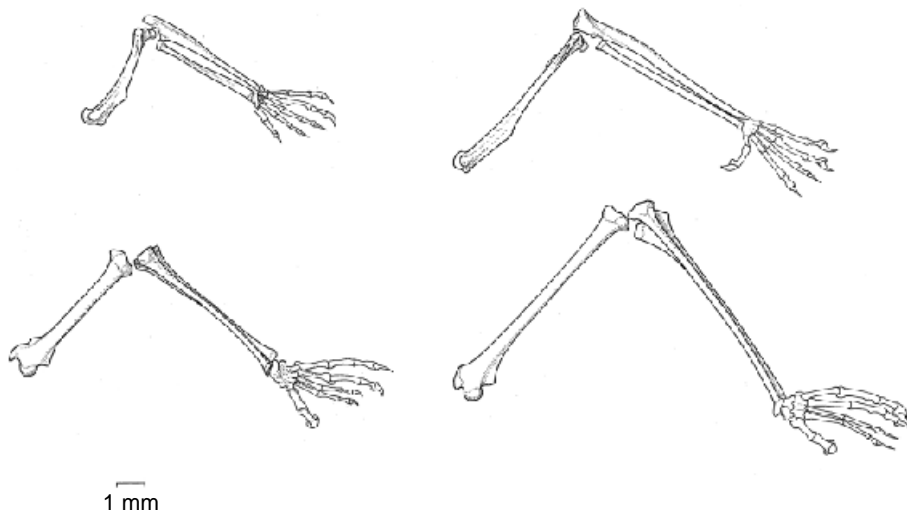
In general appearance, most petaurines and pseudocheirines have a stout body with short legs. The head is short with a pointed snout and the ears are membranous or furred on the outside. The eyes are large and protruding. The tail is long and may be tapered or bushy. Dactylopsilines are rather more slender, with a relatively large head. As mentioned above, the colour of the pelage varies widely between and, occasionally, within species. The Common Ringtail Possum shows considerable geographic variation in colour with darker forms in coastal and rainforest habitats and paler grey forms in drier inland open forests. The situation in the Greater Glider is rather different. A widespread polymorphism for coat colour extends throughout most of its range, independent of habitat type. Variants range from black with a white venter through specimens with increasing amounts of white to almost completely white individuals. The fur of most species is relatively short and fine, but longer fur is found in southern populations of Greater Gliders and Yellow-bellied Gliders. In Green Ringtail Possums the alternating bands of colour and crimped structure of the guard hairs give it a peculiar glossy green appearance.

### Body Wall

The most striking adaptation of the body wall is the possession of a patagium in *Petaurus* species and the Greater Glider. A similar development occurs in the Feathertail Glider, *Acrobates pygmaeus* (Burramyidae) and in three eutherian families: the Sciuridae, Anomaluridae and Cynocephalidae. The patagium consists of a fold of skin with the two skin layers bound together tightly by connective tissue. Through this connective tissue run numbers of muscles or individual muscle fibres which retract the patagium while not in use and control its attitude while gliding. The musculature of the patagium has been described by Johnson-Murray (1987) and differs markedly between the two genera of Petauridae and the Feathertail Glider. This suggests an independent derivation of the structure in the three groups. The Lemuroid Ringtail Possum, which is closely related to the Greater Glider, has a vestigial patagium, first noted by Cairn & Grant (1890) but ignored by subsequent authors, consisting of small flaps of skin in the axillary and inguinal regions. This species leaps from branch to branch but does not glide.

### Skeletal System

The only major adaptations of the skeletal system, other than those associated with feeding, are those found in the two gliding genera. In the Greater Glider, the long bones of the limbs are markedly elongated compared to *Pseudocheirus* of similar body weight (Fig. 28.4). The vertebrae, particularly the thoracics and lumbar, are also relatively much longer. The proximal caudal vertebrae also are elongated, resulting not only in a longer tail, but a less flexible one. While this reduces the prehensility of the tail, it increases its efficacy as a rudder during flight. The forefeet of *Petauroides* also are greatly enlarged and armed with larger claws, presumably to allow greater grasping ability when landing on a tree trunk. The Lemuroid Ringtail Possum shows these same adaptations although to a slightly less exaggerated degree.



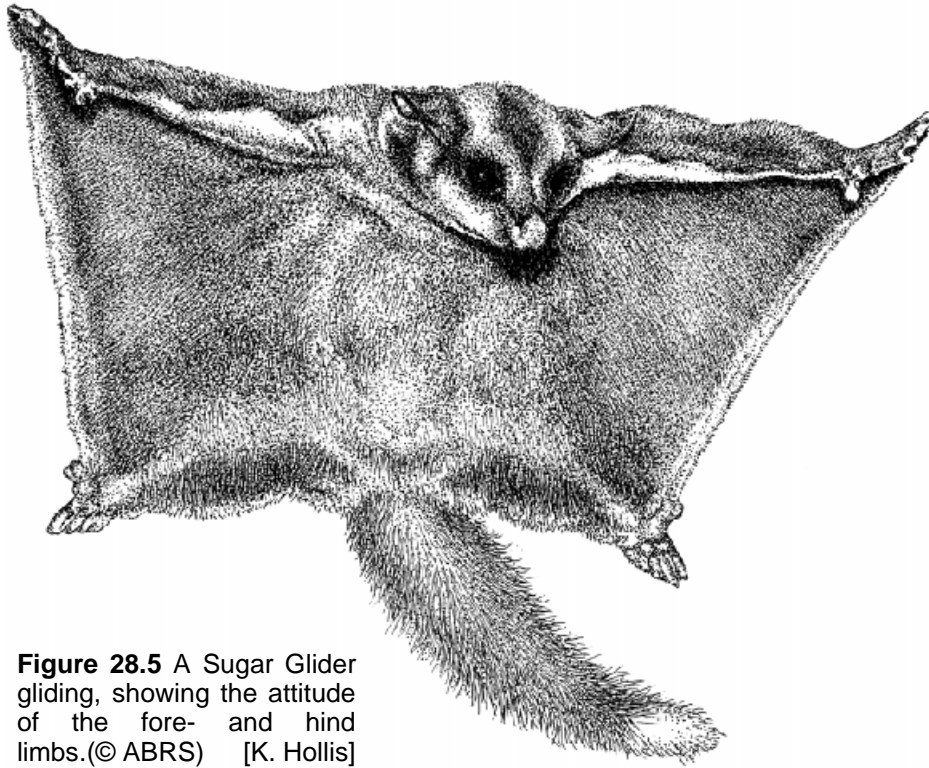
**Figure 28.4** Limb bones of the Common Ringtail Possum (left) and the Greater Glider (right) showing the elongation of the long bones and enlarged manus in the latter. (© ABRS) [S. Weidland]

The skeletons of *Petaurus* and Leadbeater's Possum show a slight elongation of the bones and virtually no elongation of the tail. Given, however, that *Petaurus* has a relatively larger patagium extending to the manus, the need for longer bones to increase the surface area to weight ratio undoubtedly is reduced.

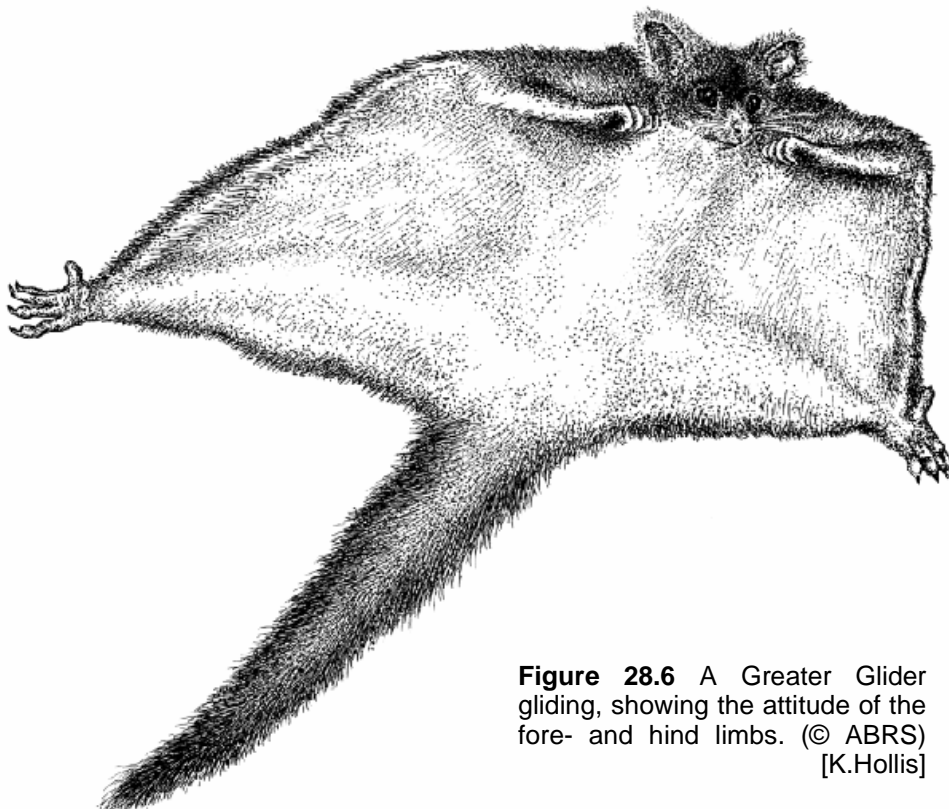
### Locomotion

The prehensile tail, opposable hallux and, in pseudocheirines, the specialised forefoot are all adaptations which allow the animal to forage on small branches and twigs. The gait of most species is the typical crossed extension walk at low speed on a flat substrate changing to a bounding gait at higher speed. In Striped Possums, however, the normal gait has been described as a 'rowing' in which diagonally opposing legs are moved simultaneously (Van Dyck 1983). In climbing vertical tree trunks the forelimbs are moved together, alternating with the hind limbs. The ability to rotate the hind foot permits head first descent of trunks. The two gliding genera show very different attitudes while airborne, as expected from the shape of the patagium described above. *Petaurus* species glide with fore- and hind limbs fully extended, the hind feet pronated and the forefeet flexed slightly upward (Fig. 28.5). The Greater Glider glides with the hind limbs fully extended, but with the forefeet tucked under the chin and the elbows extended (Fig. 28.6). Although the aerodynamics of gliding in these genera has not been studied in detail, it appears that the limbs and musculature attached to the patagium are used in both genera to control the attitude of the airfoil.





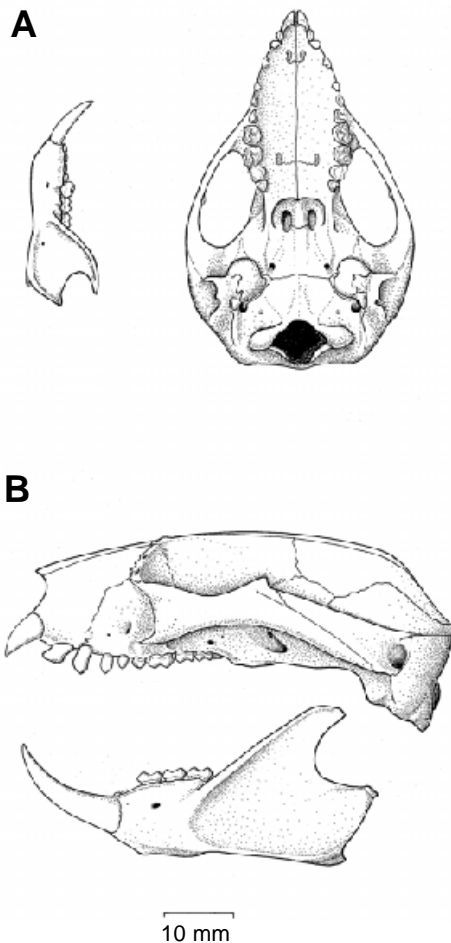
**Figure 28.5** A Sugar Glider gliding, showing the attitude of the fore- and hind limbs. (© ABRS) [K. Hollis]



**Figure 28.6** A Greater Glider gliding, showing the attitude of the fore- and hind limbs. (© ABRS) [K.Hollis]

### Feeding and Digestive System

The general features of the dentition have been described above and Figures 28.7 and 28.8 depict the detailed structure of the teeth in representatives of each subfamily. The strong incisors in petaurines and dactylopsilines are used to cut and tear bark to obtain plant exudates and insects. The Striped Possum also uses its elongated fourth digit and long tongue to help in extracting prey (Smith 1982b). The fourth digit may also be used to grasp a small branch, freeing the rest of the paw for manipulating large prey (Moeller 1976).

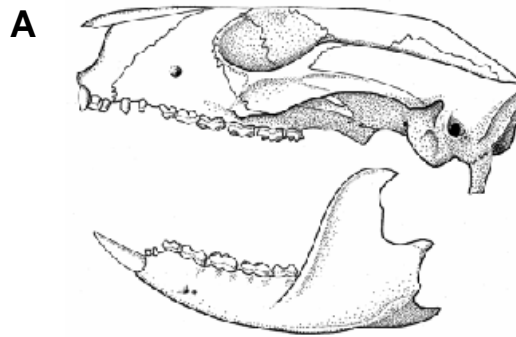


**Figure 28.7** The dentition of the Petaurinae and Dactylopsilinae: **A**, ventral view of skull of the Yellow-bellied Glider and lateral view of left dentary showing bunodont condition; **B**, lateral view of skull of the Striped Possum, showing procumbent incisors. (© ABRS) [S. Weidland]

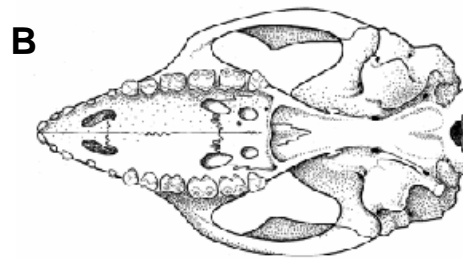
The gut of dactylopsilines is simple and adapted to a diet of arthropods. Smith (1982b) has suggested that ants and, to a lesser extent, termites may form the major part of its diet. The gut of petaurines has a relatively larger caecum and possibly may be involved in the bacterial fermentation of some plant exudates which, together with insects, are the major constituents of the diet (Hume 1982). *Petaurus* species tend to aggregate at particular feeding trees to obtain the exudates (Fig. 28.9).

Mastication has been studied in *Pseudocheirus* by Gipps & Sanson (1984) who found that natural or artificial wear of the selenodont cusps resulted in a lessened ability to reduce the particle size of ingested food. This study confirms the widely acknowledged observation that selenodontology is an adaptation for grinding fibrous food items in order to provide an increased surface area for bacterial fermentation.

The gut of pseudocheirines (Fig. 28.10) shows specialisation for fermentation of leaves, with a greatly enlarged caecum and large colon (Hume 1982). Masticated food is fermented in the caecum by the action of symbiotic bacteria.



**Figure 28.8** The dentition of the Pseudocheirinae: **A**, lateral view of the skull of the Common Ringtail Possum; **B**, occlusal view of upper dentition of the same. (© ABRS) [S. Weidland]

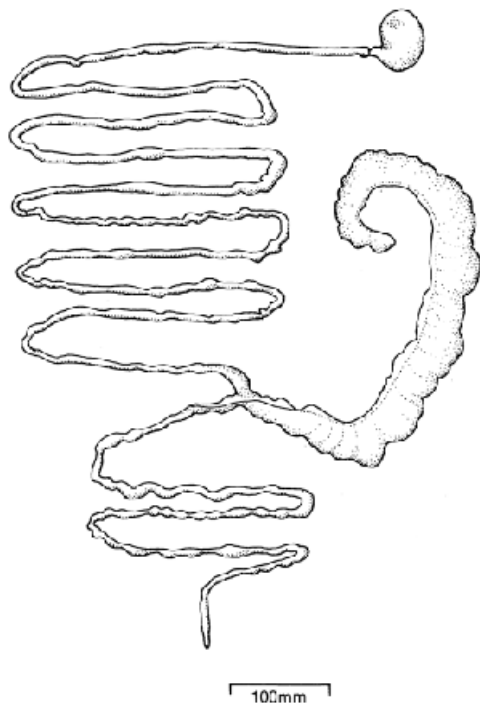


10 mm

Food is retained in the gut longer than for most other herbivores (Hume, Foley & Chilcott 1984). The fluid and fine particle components of the food are retained selectively in the caecum longer than the coarser particles. This, presumably, is a result of the lower digestibility of *Eucalyptus* foliage compared to most plants. After fermentation is complete, the contents of the caecum are evacuated as soft faeces which are reingested immediately by the animal (Chilcott 1984). The nutrient contents of these soft faeces then are absorbed on their second passage through the intestine. Such soft faeces are produced only during the animal's resting phase. Hard, completely digested faeces are produced during the active phase.

Metabolic rates for the three species studied were reviewed by Hume *et al.* (1984), who measured metabolism in the Greater Glider. Basal metabolic rates in the Sugar Glider were measured by Fleming (1980) and in Leadbeater's Possum by Smith *et al.* (1982). The latter authors also reported on energetics and water balance in free living Leadbeater's Possums. Basal metabolic rates are: Leadbeater's Possum,  $2.10 \text{ W kg}^{-0.75}$ ; Sugar Glider,  $2.31 \text{ W kg}^{-0.75}$ ; and Greater Glider,  $2.37 \text{ W kg}^{-0.75}$ . The field metabolic rate, measured on active animals under natural conditions, is 2.8 times basal metabolic rate in the Greater Glider. Nagy & Suckling (1985) reported field measurements for the Sugar Glider of 3.8 times basal metabolic rate, while the factor for Leadbeater's Possum is 5.8. Nagy & Suckling (1985) concluded this may reflect in part the efficiency of gliding as a means of locomotion. Hume *et al.* (1984) argued that the low field metabolic rate in the Greater Glider is a reflection not only of the efficiency of gliding, but is also advantageous in coping with the low nutritive value of *Eucalyptus* foliage.





**Figure 28.10** The digestive tract of the Greater Glider showing the enlarged caecum. (After Hume, 1982; © ABRS) [S. Weidland]

### Circulatory, Respiratory and Excretory Systems

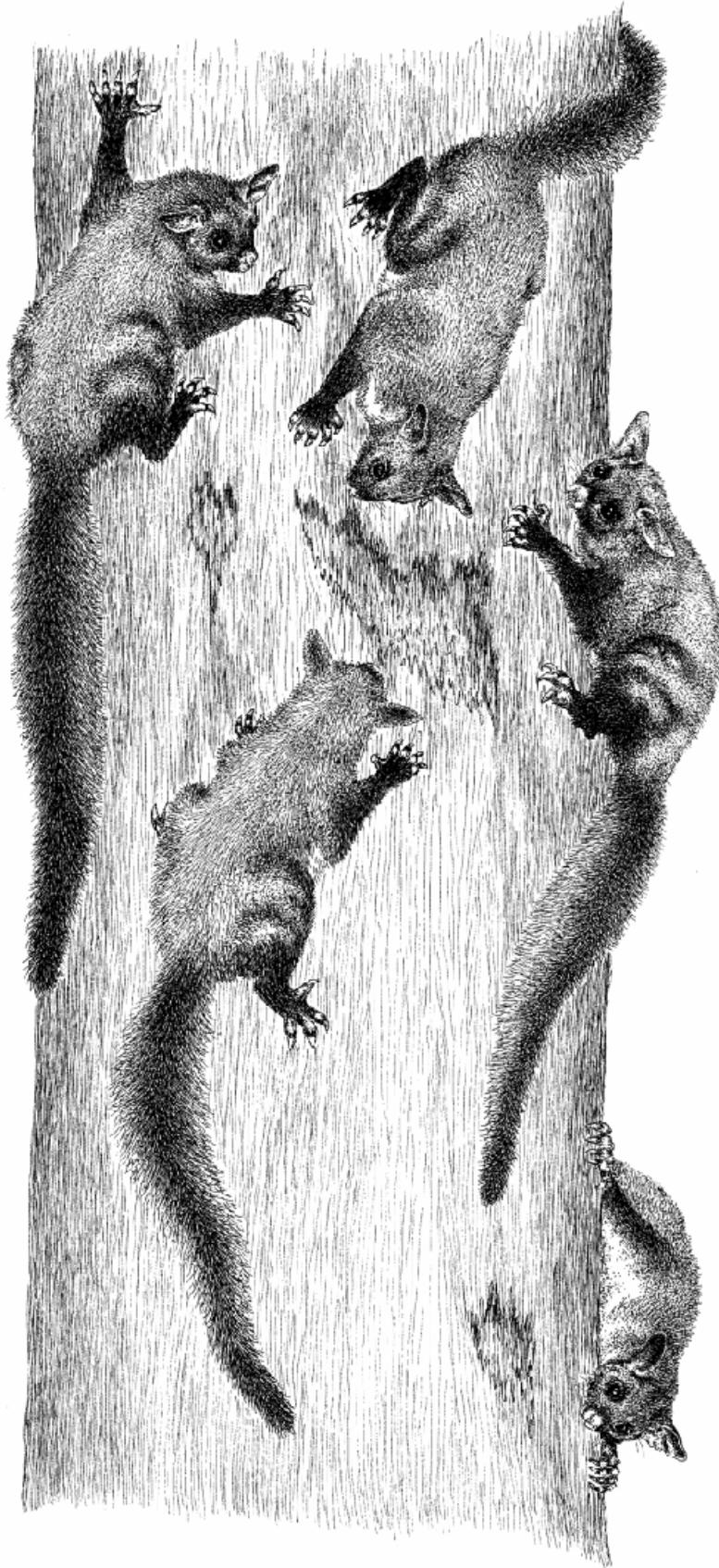
These systems have received little attention in the Petauridae. Robinson & Morrison (1957) observed *Petaurus* species distributing saliva during heat stress to increase evaporative heat loss. Since eccrine sweat glands are absent over most of the body surface in marsupials (Barbour 1977), this is probably the only method available to them of coping with extremely high temperatures.

Dawson & May (1984) studied thermoregulation in Sugar Gliders and reported a diurnal rhythm in body temperature. In the same species, Fleming (1980) described the physiology of torpor, which occurred either spontaneously or in response to food deprivation. During torpor, Sugar Gliders maintain a body temperature of 15°C or more, which is higher than in other phalangeroids which exhibit torpor. He concluded that torpor in this species is an adaptation for reducing energy expenditure during winter, when insect food is scarce and the alternative food source, *Acacia* exudates, also is limited.

Nagy & Suckling (1985) reported that Sugar Gliders obtain approximately half its water requirement from its food, the remainder presumably obtained from rainwater.

### Sense Organs and Nervous System

The nervous system and senses were reviewed by Johnson (1977) and by Biggins (1984). Petaurids show no special adaptations of the nervous and sensory systems, but they do show an interesting variation in the reflectiveness of the tapetum lucidum, a layer of pigment in the eye which reflects incident light. This is most noticeable when one searches for animals at night using a powerful torch. As this layer is reputed to increase the ability of the eye to detect low levels of light, gliding petaurids should have a strong reflection or 'eyeshine', indicating more efficient light gathering powers to help them in gliding. A strong reflection is produced by the Greater Glider and the Lemuroid Ringtail Possum, but the reflections of *Petaurus* species are among the weakest in the phalangeroids.



**Figure 28.9** A group of five Yellow-bellied Gliders feeding at a sap tree.  
(© ABRS) [K. Hollis]

Petaurids, like many other groups of mammals, possess specialised sensory hairs or vibrissae. Lyne (1959) compared the distribution and numbers of vibrissae in a number of Australian marsupials, concluding that they are most numerous in primitive and arboreal groups. Besides the mystacial vibrissae on the snout and other minor fields on the head, petaurids also have vibrissae on the limbs in the ulnar-carpal and calcaneal regions. *Pseudocheirus* species and Greater Gliders also may have a pair of vibrissae on the forearm.

### Endocrine And Exocrine Systems

The endocrine system of petaurids has received no attention, not even in the context of reproduction. There has been a number of studies on exocrine glands and their products. These are reviewed by Biggins (1984). All of the Australian species of Petauridae have at least one set of glands or glandular areas which produce odoriferous secretions. Most species possess at least one form of paracloacal gland, which is used to deposit scent on branches or trunks of trees. Such scent marks may simply serve to indicate presence of an individual or may be used to demarcate individual or group territory. Some species also possess a sternal gland which may be used in a similar manner, but in the Sugar Glider this gland is used along with the frontal gland to transfer odours between members of the social group resulting in a community-specific odour. These and other glands in this species are used to distribute individual odours or the group odour on the substrate. The Yellow-bellied Glider uses the frontal and tail glands to perform a similar function. Leadbeater's Possum creates a group odour using saliva, transferred between individuals during mutual grooming.

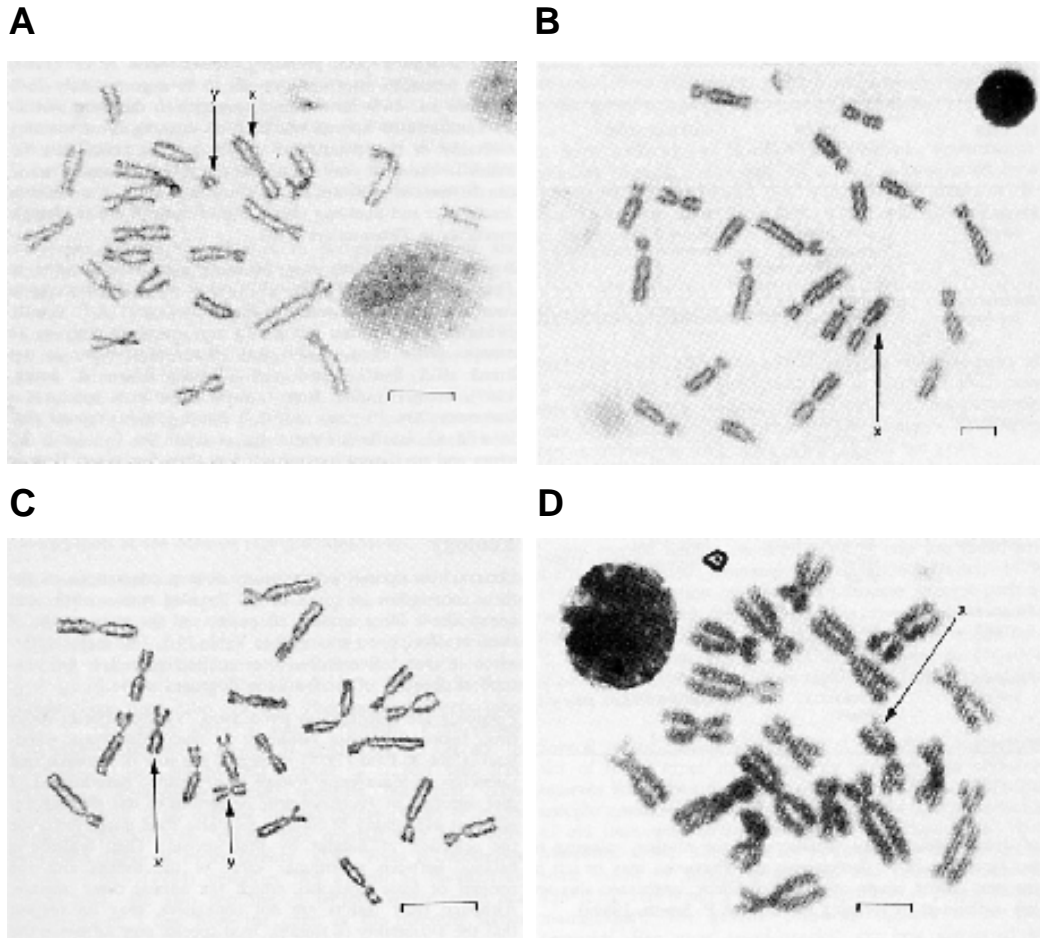
### Reproduction

The cytogenetics of the Petauridae were reviewed by McKay (1984). Diploid chromosome numbers range from 10 to 22 and sex determination is the standard mammalian XX/XY except that two species may have the sex chromosomes attached to a pair of autosomes. Supernumerary chromosomes, which vary in number from one to eight, are present in some populations of Greater Gliders. This species and the Lemuroid Ringtail Possum have two slightly different methods of selective sex chromosome elimination from somatic tissues (Fig. 28.11). In the Lemuroid Ringtail Possum, somatic tissues lack one of the X chromosomes in the female and the Y chromosome in the male, resulting in an XO condition in both sexes. In the Greater Glider, the male somatic tissues are XO, but females retain both X chromosomes.

M.J. Smith (1984a) described the reproductive systems of the Sugar Glider and Leadbeater's Possum and reviewed earlier work on pseudocheirines. The only departure from the usual marsupial condition was in the elongated lateral vaginae in the Sugar Glider. Wolffian ducts persist in the reproductive tracts of female Greater Gliders (Smith 1969). During the development of the female reproductive tract in the Common Ringtail Possum, the Wolffian ducts either disappear entirely or persist only as small caudal remnants (Armati-Gulson & Lowe 1984, 1985).

Temple-Smith (1984a) reviewed the reproductive structures and patterns in male phalangerids, confirming that they do not differ from the usual marsupial pattern. Sperm production and size of the reproductive organs is seasonal in the Greater Glider and the Common Ringtail Possum, but in some other species males may be fertile throughout the year. The ejaculate contains a large volume of prostatic fluid which may form a dense postcopulatory plug preventing insemination by more than one male.





**Figure 28.11** The chromosomes of *Petauroides* and *Hemibelideus*: **A**, fibroblasts of a male Greater Glider ( $2N=22,XY$ ); **B**, bone marrow cells from the same ( $2N=21,XO$ ); **C**, fibroblasts of a male *Hemibelideus* ( $2N=20,XY$ ); **D**, bone marrow cells from the same ( $2N=19,XO$ ). Scale lines are  $5\mu m$  in length.

Tyndale-Biscoe (1984b) reviewed the current knowledge of reproductive physiology of phalangeroids and urged that more comparative work be done. Oestrous cycle lengths are known accurately for two species: Sugar Glider (29 days) and Common Ringtail Possum (28 days). Gestation length is known only for the Sugar Glider (16 days). A.P. Smith (1984b) was unable to determine accurate durations for Leadbeater's Possum, but estimated oestrus at less than 30 days and gestation at less than 20 days. Superovulation, the production of more embryos than the teats can accommodate, has been reported in the Sugar Glider (M.J. Smith 1984a).

Reproductive patterns of petaurids were reviewed by Smith & Lee (1984). Breeding seasons generally are timed to coincide with peak food availability at weaning and vary markedly between species, from the short autumn season of the Greater Glider to the protracted breeding seasons of such species as the Yellow-bellied Glider. The Herbert River Ringtail Possum, *Pseudocheirus herbertensis*, has a major breeding season in early winter and a second, shorter summer season. Leadbeater's Possum may give birth at any season, but with peaks in autumn and spring.

## Embryology And Development

Data on early embryonic development are available only for two species, the Common Ringtail Possum (Hughes, Thomson & Owen 1965; Armati-Gulson & Lowe 1984, 1985) and the Greater Glider (Bancroft 1973). The placenta is of the choriovitelline type and intrauterine development is not different from that observed in other marsupials. Both Bancroft (1973) and Armati-Gulson & Lowe (1984) found that the reproductive tract begins development prior to differentiation of the gonad. Although the sex of neonates cannot be distinguished, the pouch or scrotum becomes visible within a few days.

Postnatal growth has been described for the Sugar Glider and the Squirrel Glider, *Petaurus norfolcensis* (Smith 1979), the Common Ringtail Possum (Hughes *et al.* 1965) and the Herbert River Ringtail Possum (Haffenden 1984). The general pattern of development follows that seen in other marsupials. Once they are able to leave the pouch, the young of *Pseudocheirus* species may remain with their mother, clinging to her fur or, as in the Herbert River Ringtail Possum and *Petaurus* species, may be left in the nest. Older young of the Leadbeater's Possum are also left in the nest by foraging mothers (A.P. Smith 1984b).

## NATURAL HISTORY

### Life History

Reproductive and life history strategies were reviewed by Smith & Lee (1984) and Lee & Cockburn (1985). Litter size in the smaller species is related inversely to maternal weight and is correlated to some extent with teat number. Species with two teats normally produce a single young and species with four teats usually have two young at parturition. The exceptions are: the Herbert River Ringtail Possum, which has two teats and regularly produces two young; the Striped Possum which also has two teats and frequently bears twins; and the Common Ringtail Possum, which has four teats and litter sizes vary from one to three.

Duration of pouch life and time to weaning depend on a combination of maternal weight and litter size, generally shorter in small females with litters of two or more and longer (up to 7.5 months to weaning in the Greater Glider) in larger species with single young (Smith & Lee 1984). How *et al.* (1984) reported that female Common Ringtail Possums, which breed twice in one year, tend to wean their first litter earlier than normal. Mortality of young prior to weaning may be extremely high in some species such as Leadbeater's Possum (A.P. Smith 1984b), and in the Sugar Glider may vary markedly between seasons from less than 20% to almost 50% (Suckling 1984). How *et al.* (1984) reported mortality rates for juveniles to be approximately 26% for male and 16% for female Common Ringtail Possums, the main mortality concentrated around the time of weaning. Post weaning mortality in this population was higher for males than females in the first year but lower thereafter. A similar trend can be seen in A.P. Smith's (1984b) data for Leadbeater's Possum and Suckling (1984) reports overall greater female mortality in Sugar Glider.

Age at first breeding may be as low as 9 months in the Sugar Glider (Smith 1973), but wild Leadbeater's Possums do not breed in their first year (A.P. Smith 1984b). Common Ringtail Possum may breed as early as 13 months (How *et al.* 1984), but Greater Gliders do not breed until their second year (Tyndale-Biscoe & Smith 1969). Longevity data from captives show most species can live more than 10 years, but A.P. Smith (1984b) reported that in wild Leadbeater's

Possums mean age at death for females is 2.9 years and maximum longevity is less than 5 years. How *et al.* (1984) reported only two female Common Ringtail Possums surviving to 6 years.

## Ecology

General descriptions of the main dietary adaptations of the three subfamilies are given above. Detailed studies of the diet are available for a number of species and the main results of these studies are summarised in Table 28.1. The major differences in diet between the three subfamilies reflect the anatomical diversity of the family as discussed above.

**Table 28.1** Diets of species of Petauridae.

SPECIES	MAIN COMPONENTS	REFERENCES
<i>Petaurus australis</i>	Arthropods <i>Eucalyptus</i> sap Nectar & manna	Henry & Craig (1984) Smith & Russell (1982)
<i>Petaurus breviceps</i>	Arthropods <i>Acacia</i> gum <i>Eucalyptus</i> sap Nectar	Smith (1982a)
<i>Gymnobelideus leadbeateri</i>	Arthropods <i>Acacia</i> gum Manna & honeydew	A.P. Smith (1984a)
<i>Dactylopsila trivirgata</i>	Formicidae Other insects	A.P. Smith (1982b)
<i>Pseudocheirus peregrinus</i>	<i>Eucalyptus</i> leaves Other leaves Fruit	Pahl (1984) Thomson & Owen (1964)
<i>Pseudochirops archeri</i>	Foliage of 22 tree species	Procter-Gray (1984)
<i>Petauroides volans</i>	<i>Eucalyptus</i> foliage	Marples (1973)

Petaurids are restricted to treed areas. Various species occur from regions of dense rainforest to open *Eucalyptus* woodland. Cork & Pahl (1984) examined the role of nitrogen and phenolics in *Eucalyptus* foliage as a possible determinant of diet selection in the Common Ringtail Possum to test the hypothesis that availability of suitable palatable food might influence the selection of habitat by that species. They indicated a balance between nutritional value of the foliage and the content of toxic phenolics which the animal must tolerate. Although their results were not conclusive, they did suggest that the availability of suitable food species may influence the abundance or even presence of animals in a particular area.

Winter's (1984a) study of the distributions of petaurids in northern Queensland provided valuable data on the habitat requirements of a number of species. Several species have restricted altitudinal as well as geographic ranges, correlated with particular plant associations. *Pseudocheirus* species inhabit quite different vegetation types. Although they overlap broadly geographically, they do not compete for the same resources. The Yellow-bellied Glider and the Sugar Glider also overlap in range, but the former is restricted to a few areas of tall forest while the latter is more broadly distributed. The data presented by Braithwaite (1983) show a similar pattern in the distributions of these two species in southern New South Wales. Little is known of the ecology of the Squirrel Glider, but it appears to prefer drier inland areas than its congeners (Suckling 1983).



Speare *et al.* (1984) reported on a number of diseases and parasites from the Striped Possum, the Lemuroid Ringtail Possum, the Herbert River Ringtail Possum, and the Green Ringtail Possum. Endoparasites include Protozoa and a variety of Cestoda and Nematoda. Ectoparasites reported are fleas of the family Pygiopsyllidae and ticks of the family Ixodidae. Mites of the family Laelapidae were also recorded from a variety of petaurids (Domrow 1966). Pygiopsyllid fleas have been reported from a number of petaurids (Dunnet & Mardon 1974), but lice (Phthiraptera) do not occur (Calaby 1970).

Although domestic cats are notorious for bringing young possums (*Petaurus* species and *Pseudocheirus* species) home to their owners, comparatively little is known of the predators of petaurids. Fleay (1968), however, described cases of predation on a number of species by the Powerful Owl, *Ninox strenua*, and Estbergs & Braithwaite (1985) recorded Sugar Gliders as a prey item of the Rufous Owl, *Ninox rufa*. Robertshaw & Harden (1985a) reported that Common Ringtail Possums and Greater Gliders are eaten occasionally by dingoes in New South Wales.

Yellow-bellied Gliders, which live in polygynous groups and occupy a group den, share their group home range (Henry & Craig 1984; Russell 1984) but tend to forage independently. Russell (1984) found only minimal overlap between home ranges of adjacent groups. A similar pattern is exhibited by Sugar Gliders (Henry & Suckling 1984). Adults of this species attack intruders. Leadbeater's Possums (A.P. Smith 1984b) have a different social organisation. The basic unit consists of a monogamous pair plus one or more generations of offspring and, occasionally, additional unrelated adult males. These groups, which are termed colonies, occupy exclusive home ranges. Males may move between colonies, but females which move are more likely to be wandering transients. In any colony only one female will reproduce. Dispersal of both adult and juvenile animals was frequent and the composition of the colonies changed constantly.

The pseudocheirines show a variety of patterns of sociality (solitary to small groups), but none are as complex as in the petaurines. Winter & Atherton (1984) described social groupings in four pseudocheirine species. The Green Ringtail Possum is solitary. The only long term association is between mother and young. The young of this species is dependent for a longer time than other species. Herbert River Ringtail Possums and Common Ringtail Possums show a similar pattern. Lemuroid Ringtail Possums, occur in groups of up to six individuals. These groups may consist of a pair and their offspring. Greater Gliders occupy individual home ranges. There is no overlap between home ranges of males, although female home ranges may overlap with each other and with those of males (Henry 1984; Kehl & Borsboom 1984). Henry (1984) described this system as facultatively polygynous. He also described a pattern where male and female share a den from the onset of the breeding season until the young emerge from the pouch.

## Behaviour

Many aspects of behaviour have been dealt with in earlier sections, but two areas deserve further mention.

Petaurids such as the Sugar Glider, studied by Goldingay (1984), are strictly nocturnal, presumably in order to avoid diurnal predators. The Green Ringtail Possum, however, is occasionally active in daytime (Winter & Atherton 1984). In the wild, most species tend to emerge at or shortly after dusk and may spend some time in the den tree or, as in the case of the Yellow-bellied Glider, move rapidly away (Russell 1984).

Biggins (1984) reviewed communication in phalangeroids. Two of the primary means of communication between group members in the social species are olfactory and vocal.

In *Petaurus* species, olfactory communication appears to serve primarily to produce a group odour which is used to mark areas used by members of the group to exclude other groups. Vocalisations, which are highly variable, occur in a number of social contexts, including the loud flight call of the Yellow-bellied Glider. Mutual grooming by group members is another common form of communication in these species, frequently associated with transfer of scent and occurs when two group members meet.

The pseudocheirines are less vocal, the two main contexts are during agonistic encounters and when an infant becomes separated from its mother. Odours are used by most species in this group primarily for marking the substrate.

In most petaurids, as in other phalangeroids, agonistic encounters between individuals usually are accompanied by a stereotyped display where the animals stand erect on the hind limbs with forelimbs spread widely and utter a rasping or hissing call.

### Economic Significance

Petaurids have little economic importance either as pests or in controlling pests, presumably as a result of their very specialised dietary requirements. Occasionally *Pseudocheirus* species may be a minor pest in orchards. The petaurids have never been exploited for their hides, which do not tan easily.

Most species are relatively common in the areas where they do occur. The exception is Leadbeater's Possum which has a very restricted range. Although common, petaurids are still vulnerable to the effects of logging and fire. Many have highly specific habitat requirements and now are found primarily in isolated remnants of vegetation (Winter 1979, 1984a). This situation requires that adequate reserves such as national parks and forest reserves be maintained to ensure their continued survival. The species most at risk in Australia is Leadbeater's Possum. Though adapted to surviving succession following fire, it is highly vulnerable to modern logging regimes (Smith 1983).

Several recent studies have aimed at identifying characteristics of forest types that constitute adequate and sufficient reserves for petaurids (Davey 1984; Kavanagh 1984) and specific considerations such as the need for the preservation of old trees with cavities for nest sites (Mackowski 1984; Meredith 1984). The need for nesting holes can be met to some extent by supplying artificial nest boxes (Menkhorst 1984), but this is not a preferred alternative to proper habitat management. The general consensus appears to be that petaurids, like most small species, are best conserved by conserving large areas of their preferred habitat.

Petaurids can be studied in the field using a battery powered torch masked with red cellophane (Russell 1984), which allows the observer to follow their activities with minimum disturbance.

Because petaurids are primarily arboreal, conventional methods of collecting small mammals are not appropriate. A number of ingenious methods have been devised by workers studying behaviour and ecology in the wild. Placing wire mesh traps on brackets nailed to the trunks of either feeding or nest trees (Henry & Craig 1984; A.P. Smith 1984b) and the construction of artificial horizontal branches (A.P. Smith 1984b) are efficient methods of capturing *Petaurus* species and Leadbeater's Possum. Kehl & Borsboom (1984) were able to capture and mark Greater Gliders by shooting off the branch on which the animal was feeding, forcing the animal to glide to the ground. Some *Pseudocheirus* species individuals which feed or nest in lower vegetation simply can be shaken to the ground (Haffenden 1984; How *et al.* 1984).

For studies of behaviour, movements and home range on wild populations, various petaurids have been marked with reflective ear tags (Henry 1984) or with radio transmitters attached by a collar and a reflective tail tag (Kehl & Borsboom 1984).

## BIOGEOGRAPHY AND PHYLOGENY

### Distribution

In Australia, petaurids occur in coastal areas from southern South Australia around the eastern and northern coasts to the Kimberley region. Some species extend inland to the limit of open woodland. An isolated population of *Pseudocheirus* species occurs in the south-western tip of Western Australia. Within this broad area, some genera and species have a wide distribution while others may be restricted to a small area of a particular vegetation type. Examples of generalists which occur in a variety of habitat types are all Australian *Petaurus* species, the Common Ringtail Possum, and the Greater Glider. Leadbeater's Possum is restricted to the *Eucalyptus regnans* forests of central Victoria. The Striped Possum occurs only along the east coast from Cape York to Mt Spec. The Lemuroid Ringtail Possum and the Herbert River Ringtail Possum inhabit the montane rainforests from Mt Spurgeon to the Cardwell Range. The Green Ringtail Possum occurs over a wider range of altitudes, but only between the Mt Windsor Tableland and Mt Spec. The Rock Ringtail Possum, *Petroseudes dahli*, is found only in certain isolated areas of sandstone escarpment in northwestern Australia.

Outside Australia, petaurids occur only on New Guinea (including Irian Jaya) and some of the adjacent islands including Salwatti and Japen; Aru and Fergusson (*Dactylopsila* species and *Petaurus* species); Waigeu (*Dactylopsila*); Batchian, Mysol, Owi, Biak, New Britain and the D'Entrecasteaux Islands (*Petaurus*) (Laurie & Hill 1954). As with the Australian species, some of the New Guinean forms are distributed widely while others are restricted to a single mountain range or habitat (Ziegler 1977).

In both Australia and New Guinea, the main factors which determine the limits of distribution of particular species appear to be related to diet. Most petaurids are highly specialised feeders and the distribution of these specialists is correlated closely with the distribution of the main components of their diet. The only apparent exception to this is the Rock Ringtail Possum, which appears to be restricted more by the availability of rocky escarpments for refuge. The fossil record shows that relatives of many forms were formerly more widespread during periods of more mesic climates. The present distribution of most petaurids in an arc around the rim of the continent can be attributed directly to the formation of refugia as the climate became more arid. One probable exception to this might be the Striped Possum, possibly a fairly recent invader from New Guinea.

### Affinities within the Petauridae

Morphologically, the Petauridae is more diverse than any other family in the Marsupialia. This is emphasised above in the description of the feeding and digestive system and is confirmed by a number of other lines of evidence. The karyotypes of petaurines and the Striped Possum show no apparent relationship to each other or to those of pseudocheirines, though all three groups may be derived from a common ancestral form (McKay 1984). Immunological distances between various petaurids and other phalangeroids show even more strikingly the lack of a special relationship within this family. Baverstock (1984) presented data which show that the Petaurinae are related more closely to the Tarsipedidae and some Burramyidae than to the Pseudocheirinae, although all of these are related more



closely to each other than to the Phalangeridae. He concluded that the Petaurinae are probably the sister group of the Pseudocheirinae, but did not address the question of family status. Given that much work is still to be done on these groups and their relationships, a conclusion is not possible.

Within the Petaurinae, the genus *Petaurus* appears to be a monophyletic group closely related to *Gymnobelideus* and *Dactylopsila* is related to *Petaurus*, but not closely (Baverstock 1984). All four Australian *Petaurus* share a common karyotype which appears to differ from *Gymnobelideus* by a series of inversions, but the karyotype of *Dactylopsila* cannot be compared easily without further study (McKay 1984).

In the Pseudocheirinae, *Hemibelideus* is related more closely to *Petauroides* than to *Pseudocheirus* (McQuade 1984). These three appear to form a monophyletic group separate from *Pseudochirops* (Archer 1984b; McKay 1984). Immunological data indicate that the probable time of divergence between *Pseudocheirus* and *Petauroides* was in the order of 25–30 mybp (Baverstock 1984).

### Fossil Record

The fossil record of petaurids was briefly reviewed by Archer (1984b). Petaurines are poorly represented in the Australian fossil record. The only Tertiary record is a specimen attributed to *Petaurus*. Dactylopsilines are not reported. Pseudocheirines have a slightly better representation. The earliest specimens occur in the Middle Miocene in several localities. These specimens reveal that the radiation into separate *Pseudocheirus* and *Pseudochirops* lineages already had begun. By the Early Pliocene, specimens referable to *Petauroides* had appeared, as had a now extinct lineage including the genus *Pseudokoala*. This evidence of an early radiation of the Pseudocheirinae strongly supports similar conclusions from immunological studies. There are records of as yet unnamed giant Pleistocene pseudocheirines. The latter parallel gigantism in other families.

## MAINTENANCE IN CAPTIVITY

Petaurids have been maintained in captivity in cages which vary markedly in size from as small as 0.33 m<sup>3</sup> for Common Ringtail Possums (Presidente 1982a) to 429 m<sup>3</sup> for Herbert River Ringtail Possums (Haffenden 1984). Collins (1973) and Dunn (1982) strongly recommended the use of cages that are as large as possible, with branches supplied, to permit the animals space to move around. Adequate space to permit gliding also is recommended for both *Petaurus* species and Greater Gliders.

Because most petaurids have relatively specialised dietary requirements, the diet offered in captivity should closely follow the types of food normally chosen in the wild. Artificial diets much favoured by many Northern Hemisphere zoos should be avoided. Petaurines can be maintained on a mixed diet of fruit, blossoms and insects although alternative sources of animal protein can be used. Dactylopsilines should be fed a higher proportion of animal protein. Pseudocheirines, which are all dependent on bacterial fermentation, should be fed on the leaves and blossoms of their normal food trees; some fruit may be offered occasionally.

Presidente (1982a) and Speare *et al.* (1984) summarised the pathologies reported from a variety of species and both report stress as one of the major contributing factors to illness in captives. Some of this stress might be avoidable

if cage size is increased, adequate branches are supplied and attention is paid when housing animals to their normal pattern of social organisation (Collins 1973).

## CLASSIFICATION

The Petauridae is currently being revised, but at present the family is considered to consist of seven genera and 23 species divided into three subfamilies.

The subfamily Petaurinae contains two genera, one of which is monotypic and the other contains five species. Species in Australia are *Gymnobelideus leadbeateri*, *Petaurus australis*, *P. breviceps*, *P. norfolcensis*, and the Mahogany Glider, *P. gracilis*. *Petaurus breviceps* also occurs in New Guinea as does *P. abidi*.

The Dactylopsilinae consists of a single genus containing four species. *Dactylopsila trivirgata* occurs both in New Guinea and Australia, but *D. megalura*, *D. tatei* and *D. palpator* are restricted to New Guinea.

The Pseudocheirinae is the largest subfamily with four genera and fourteen species. *Hemibelideus lemuroides* and *Petauroides volans* are limited to Australia. The two Australian members of the genus *Pseudocheirus* are *P. herbertensis* and *P. peregrinus*. *Pseudocheirus canescens*, *P. caroli*, *P. forbesi*, *P. mayeri* and *P. schlegeli* occur in New Guinea. *Pseudocheirops archeri* and *P. dahli* are the two Australian representatives of this genus. Three remaining species, *P. albertisii*, *P. corinnae* and *P. cupreus*, occur in New Guinea.

## DESCRIPTIONS OF INCLUDED TAXA

Diagnostic characters and descriptions of the three subfamilies are given under the general family descriptions above. The following descriptions provide diagnostic characters for the genera.

### Subfamily Petaurinae

*Gymnobelideus*: Grey above with a darker median dorsal stripe, pale below, tail grey; hairs on the tail longer distally; claws small; patagium absent.

*Petaurus*: pale grey to dark grey above with dark median dorsal stripe, pale grey to white below, tail generally darker distally; hairs on tail long, sometimes more bushy proximally; claws large; patagium present, extending from forefoot to hind foot.

### Subfamily Dactylopsilinae

*Dactylopsila*: as for the subfamily: prominent black and white longitudinal stripes; fourth digit of manus elongated.

### Subfamily Pseudocheirinae

*Hemibelideus*: grey-brown above without median dorsal stripe, yellowish below; tail long, bushy, evenly furred with short naked area at tip only; ears small, furred on outer surface; patagium vestigial.

*Petauroides*: fur long, varying from black to pale grey above, white or whitish below; tail long and evenly bushy with small naked patch ventrally at tip; ears large with long fur on outer surface; patagium present, extending from elbow to tibia.

*Pseudocheirus*: fur short, widely varying in colour, but generally paler below, median dorsal stripe present or absent, often a white patch behind the ear, distal third to half of tail always white; tail approximately same length as head and body and tapered with fur progressively shorter distally, long distal ventral friction pad; pupil circular.

*Pseudochirops*: fur short, dense and fine, grey or greenish above, paler below, dark median dorsal stripe or two pale stripes; tail shorter than head and body, tapering rapidly from a thickly furred base to sparsely furred tip, friction pad long; pupil a vertical slit.

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