



FAUNA *of* AUSTRALIA

24. PERAMELIDAE

G. GORDON & A.J. HULBERT



Western Barred Bandicoot—*Perameles bougainville* [F. Knight/ANPWS]



Pig-footed Bandicoot—*Chaeropus ecaudatus* [F. Knight/ANPWS]

DEFINITION AND GENERAL DESCRIPTION

The Peramelidae is distinguished from other polyprotodonts by the fusion of digits II and III of the hind feet (syndactyly), a condition more characteristic of diprotodonts. The family is distinguished from diprotodonts by the dentition, particularly by the presence of three pairs of lower incisors, in contrast to the single prominent pair in diprotodonts. These characters collectively separate the superfamily Perameloidea from all other marsupials. Peramelids differ from members of the other family of bandicoots, the bilbies (*Thylacomyidae*), by possessing shorter ears (less than about 60 mm; bilbies about 60–110 mm), shorter hair with slightly stiff to very stiff guard hairs (bilbies with long silky hair) and a shorter tail with short hair or short crest (bilbies with relatively longer tail and longer hair).

Peramelids are small marsupials with a long pointed muzzle; they are usually stockily built, with short limbs and neck (Fig. 24.1). The head and body length is 150–560 mm, tail length 120–340 mm and weight about 200–4700 g. Teeth are small, relatively even-sized and pointed, as in typical insectivore teeth (Fig. 24.2). The bandicoot body is basically designed for digging in soil to extract invertebrate food. The elongate muzzle and powerful foreclaws are used for probing in crevices and rooting and digging in soil.

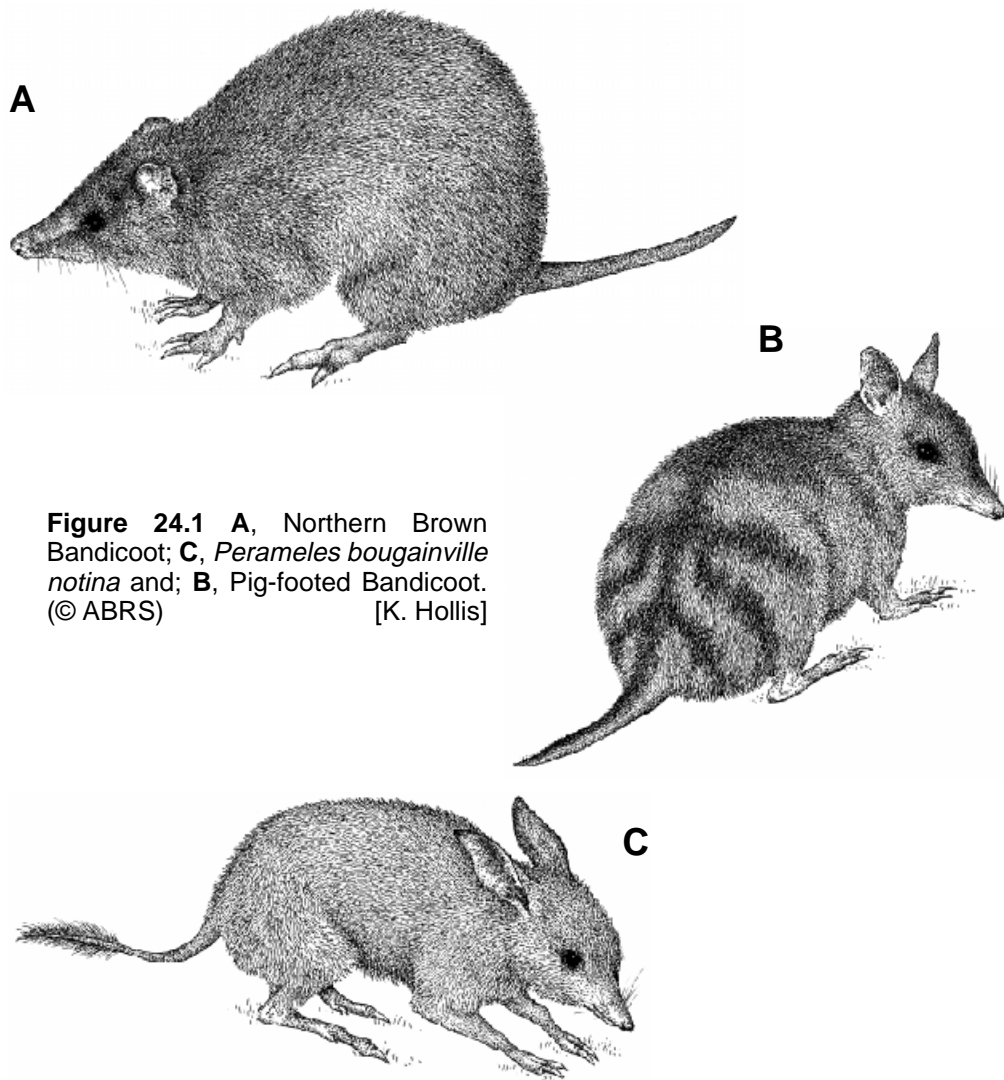


Figure 24.1 A, Northern Brown Bandicoot; C, *Perameles bougainville notina* and; B, Pig-footed Bandicoot. (© ABRS) [K. Hollis]

The tail is one-quarter to one-half the length of the head and body. The forelegs are shorter than the hind legs, usually thickset, usually with digits II, III, IV prominent and with strong flattened claws and digits I and V reduced to stubs (Fig. 24.3). The Pig-footed Bandicoot, *Chaeropus ecaudatus*, has only digits II and III prominent and functional (hence the common name); digit IV is a minute stub and apparently non-functional, and the others are absent. The hind foot is elongate, digit I reduced to a small stub, digits II and III form a syndactylous comb, digit IV greatly elongated to form main foot pad and digit V usually much shorter than digit IV (Figs 24.3 & 24.4). The Pig-footed Bandicoot lacks digit I entirely and has digit V reduced to a small, apparently non-functional stub. Thylacomyids also lack digit I.

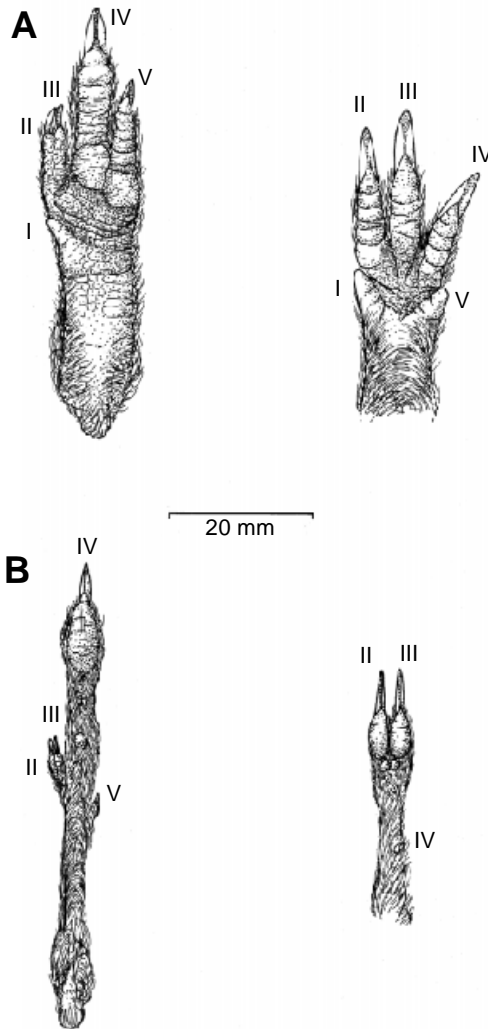


Figure 24.3 Ventral view of forefoot (right) and hind foot (left) of **A**, Northern Brown Bandicoot and **B**, Pig-footed Bandicoot. I-V = digits one to five, respectively. (© ABRS) [T.G. Cochran]

The pouch opens to the rear, usually with eight nipples, occasionally with six (Tate 1948).

The dental formula is usually I 1-5/1-3 C 1/1 PM 1-3/1-3 M 1-4/1-4.

Echymipera and *Rhynchomeles*, however, differ from all other bandicoots in that the number of upper incisors is reduced to four pairs. The last lower incisor always has a bifid crown.

The molars are multicuspid, with the four principal cusps derived from the paracone, metacone, protocone and hypocone (Rich 1982). In bilbies, the four principal cusps are derived from the two styler cusps and the protocone and metacone (Fig. 24.5). The metacone in bilbies occurs closer to the internal side of the tooth, the paracone is smaller and the hypocone greatly reduced or absent (Rich 1982).

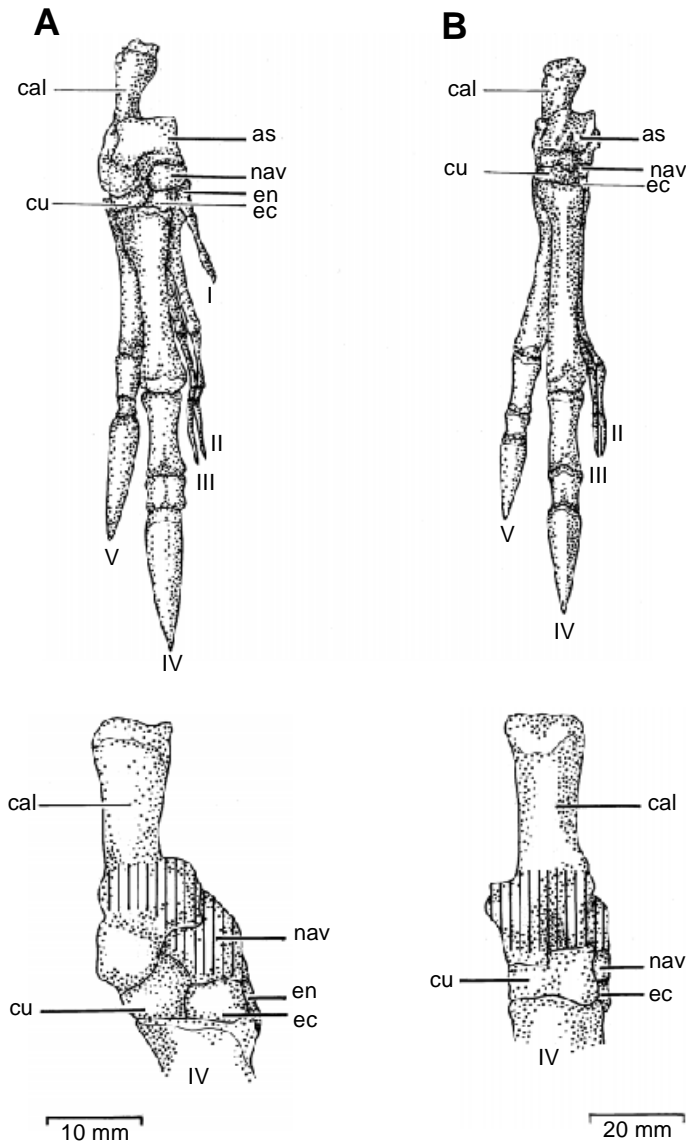


Figure 24.4 Structure of hind foot of **A**, *Perameles* and **B**, *Macropus*. I-V = digits one to five, respectively. as = astragalus; cal = calcaneum; cu = cuboid; ec = ectocuneiform; en = entocuneiform; nav = navicular. (Modified after Marshall, 1972). Vertical hatching shows areas of contact of the astragalus with the navicular and calcaneum (astragalus removed). In *Perameles*, the contact of the astragalus with the navicular is relatively greater and the contact with the calcaneum is relatively smaller than in *Macropus*. *Perameles* also shows contact of the navicular with the proximal end of the cuboid. (© ABRS) [T.G. Cochran]

Gestation lasts 12.5 days in at least some species. A chorioallantoic placenta is formed in addition to a yolk-sac placenta (Fig. 24.8). Females are polyoestrous in at least some species and appear to be able to breed whenever conditions are favourable.

A high reproductive rate can be attained in favourable conditions because of the short gestation, rapid development of pouch young, minimal parental care, early sexual maturity and rapid litter succession in the polyoestrous females.

Sperm morphology is distinctive (Hughes 1965). The sperm head exhibits dorso-ventral flattening and has concave lateral margins. The acrosomal material occurs as a proximal cap and the ventral groove runs along the entire ventral surface.

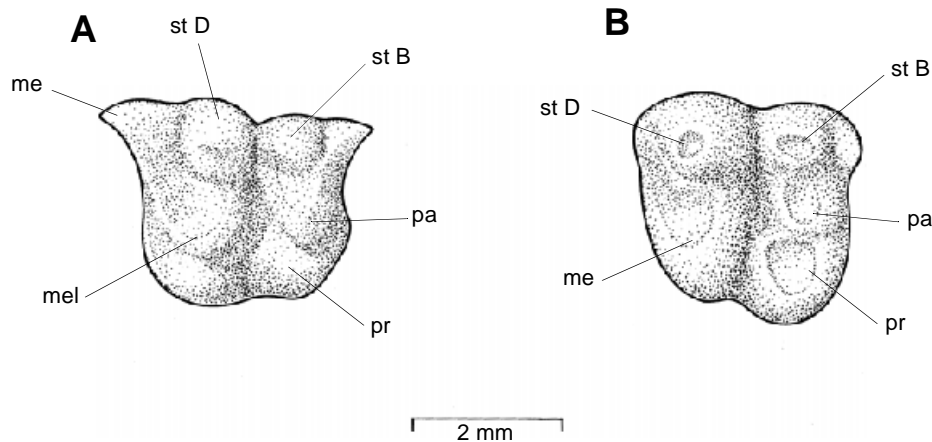


Figure 24.5 Molar cusps of **A**, Northern Brown Bandicoot and **B**, Bilby. me = metacone; mel = metaconule (hypocone); pa = paracone; pr = protocone; st B = stylar cusp B; st D = stylar cusp D. (Modified from Rich 1982) (© ABRS) [G. Milledge]

HISTORY OF DISCOVERY

The first bandicoots described from Australia came from the Sydney region, the site of first European settlement. Europeans reaching Australia prior to the arrival of the First Fleet either overlooked bandicoots or thought them too unremarkable to collect. The Southern Brown Bandicoot, *Isoodon obesulus*, was the first species to be described, in 1797 by Shaw (as *Didelphis obesula* or the Porculine Opossum, see Dixon 1981). As with so many early collections, the precise locality is unknown, but there is a strong probability that the type specimen came from the Sydney region (Dixon 1981). The Long-nosed Bandicoot, *Perameles nasuta* followed in 1804, collected by the French Baudin expeditions to south-eastern Australia. The locality is again unknown, although it is thought to be the Sydney region (Tate 1948).

Most other bandicoots were collected either as a result of voyages of exploration or during early settlement of new regions. By the end of the 19th Century, all of the currently recognised Australian species had been obtained, with the exception of the Rufous Spiny Bandicoot, *Echymipera rufescens*. This species was collected from New Guinea in 1873, but not from Australia until the zoogeographer P.J. Darlington discovered it on Cape York Peninsula in 1932 (Tate 1952b).

Collection of some important populations or subspecies also carried over into the 20th Century - *Isoodon obesulus barrowensis* from Barrow Island by Tunney in 1900, *I. o. nauticus* from Nuyts Archipelago, South Australia, by Jones in 1922 and *I. o. peninsulae* from Cape York Peninsula by R. Kemp in 1912. The anthropologist/zoologist Donald Thomson in the 1920s and 1930s (Dixon & Huxley 1985) and the Archbold Expeditions of 1948 (Tate 1952b) provided more records of the latter subspecies, which subsequently has proved difficult to locate.

A fortunate result of the early collecting was the discovery of a number of populations from various localities where species are now extinct. Semi-arid and arid zone bandicoots have declined drastically and the only records of species and their biology in many areas comes from these early collections. The Pig-footed Bandicoot, now thought to be extinct, was mainly recorded by the explorers Mitchell and Grey and the naturalists Baldwin Spencer, Gilbert and

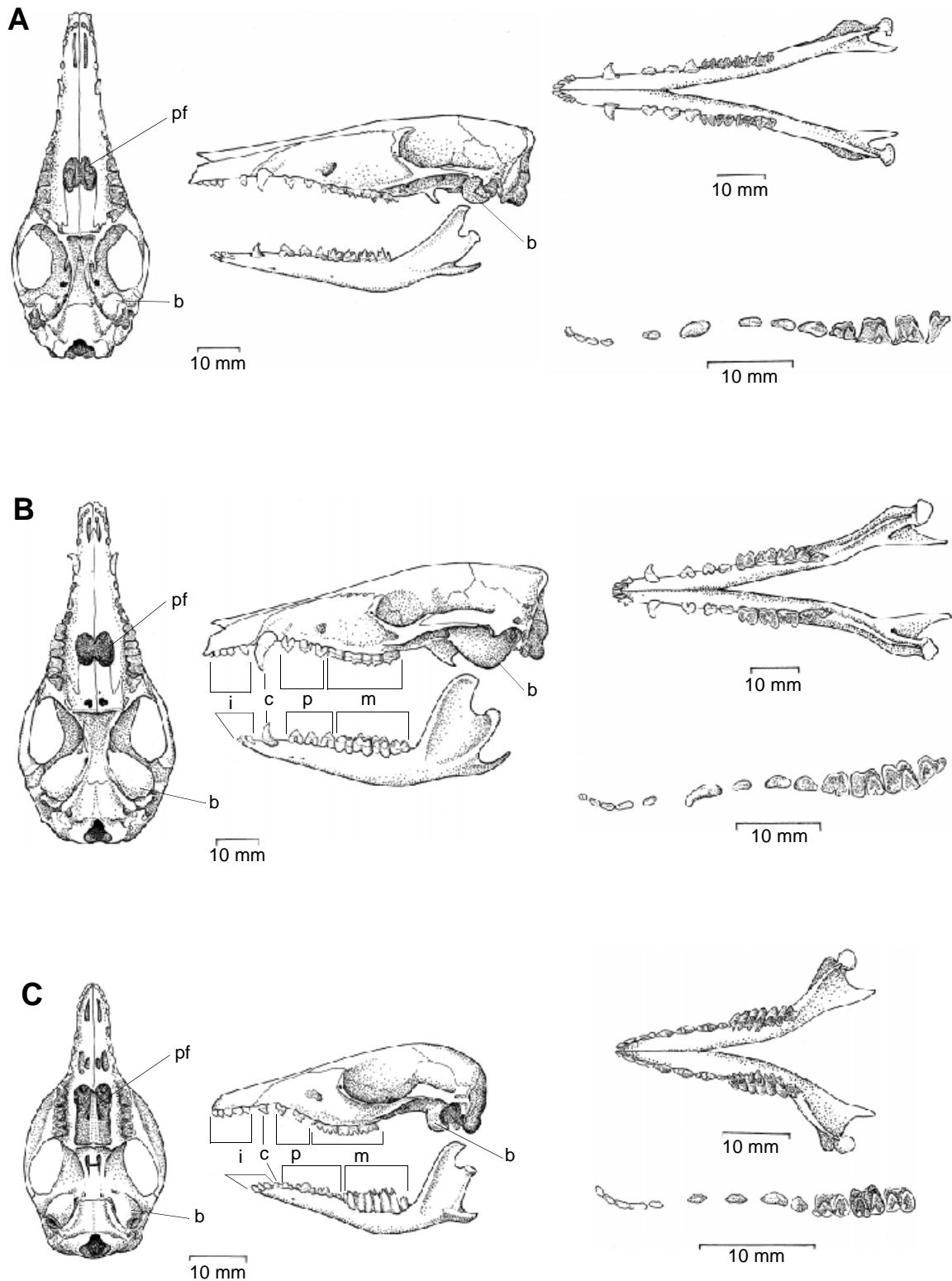


Figure 24.2 Cranium, mandible and upper toothrow of **A**, Long-nosed Bandicoot; **B**, Northern Brown Bandicoot and **C**, Pig-footed Bandicoot. b = bullae; c = canine; i = incisors; m = molars; p = premolars; pf = palatal foramina. (© ABRS) [S. Weidland]

Krefft. The first specimen was collected by Thomas Mitchell in 1836, was tail-less, hence the specific name *ecaudatus*. When Gerard Krefft attempted to collect it on the lower Murray in 1857, he ‘was in the habit of showing a copy of Sir Thomas Mitchell's tail-less specimen to the natives, urging them to procure animals of that description’ (Krefft 1866). As a consequence, the Aborigines did not recognise it as a ‘Landwang’, the native name for the species in the region, and supplied a large number of the common Southern Brown Bandicoot, with the tail removed.

Baldwin Spencer's collectors, Gillen and Byrne, obtained the first specimens of the Desert Bandicoot, *Perameles eremiana*, in the 1890s and only a handful have since been found. The Golden Bandicoot, *Isoodon auratus*, and the Western Barred Bandicoot, *Perameles bougainville*, species group, now greatly reduced, also were recorded by early collectors, apparently sufficiently well to document the broad extent of their distributions. These include collections by Daisy Bates and Jones from the Nullarbor and O.H. Lipfert on the Canning Stock Route.

Aborigines apparently played an important role in early collecting and may actually have done all the hard work of finding and capturing the animals for nearly all collectors. When Krefft finally obtained his Pig-footed Bandicoot, he had to pay the native collectors a higher than normal price on account of its rarity in the district (Krefft 1866). Byrne described how Aborigines in central Australia collect Desert and Pig-footed Bandicoots (Spencer, 1897):

‘the Iwurra (Desert Bandicoot) and Tubaija ... (Pig-footed Bandicoot) are almost identical in their habits, and build similar nests of grass and twigs in shallow oval hollows scooped out in the ground. They are captured in the same way, viz., by placing one foot on the nest, pinning the animal down and then pulling him out with the hand’.

The bilbies required a different approach:

‘whilst the Urgata ... (Bilby, *Macrotis lagotis*) occupies the inner end of his burrow the Urpila (*M. leucura*) during the winter months lies within a foot or so of the entrance of his and only uses the inner chamber during the summer. This peculiarity is taken advantage of by the natives who jump on the surface of the ground behind the Urpila breaking it in and so cutting off his retreat to the inner chamber. He is thus compelled to rush out through the entrance where a native is waiting to give him his quietus. The Urgata cannot be captured in this way and has to be dug out’.

Aborigines aided other early bandicoot collectors (Dahl 1897; Dixon & Huxley 1985; Finlayson 1935a) and with their intimate knowledge of the ecology and behaviour of the fauna were probably essential to the success of bandicoot collecting. Without their efforts, our knowledge of the status and biology of bandicoots at that time would have been much poorer.

Important collections of Australian bandicoots are held by most Australian museums. The collections of the South Australian Museum and the Museum of Victoria are particularly important for the arid and semi-arid species. The British Museum (Natural History) has good collections of some groups including the *Perameles bougainville* group and *Isoodon obesulus peninsulae*.

The name ‘bandicoot’ comes from the Telegu language word ‘pandi-kokku’ or pig-rat, referring to a large rodent, *Bandicota indica*, of the eastern Deccan plateau, southern India. The first known use in Australia was by the explorer Bass in 1799 (Jaeger 1955; Troughton 1954; Walker 1975).

From early times, perameloids were recognised as a distinct and cohesive group. The family name, Peramelidae, was used as early as 1838 by Waterhouse. For many years it included the bilbies (*Macrotis*, Thylacomyidae) although some authors recognised the distinctiveness of the latter group (Rich 1982) as shown

by dental, serological and chromosomal characters (Bensley 1903; Hayman & Martin 1974; Kirsch 1977a; Martin & Hayman 1967). Archer & Kirsch (1977) proposed a separate family, Thylacomyidae, which has been used by Kirsch & Calaby (1977) and subsequent authors (Strahan 1983).

Recently, however, Groves & Flannery (1990) have proposed a different division of the perameloids into two families: Peroryctidae, containing all New Guinea (predominantly rainforest) species, and Peramelidae, containing all Australian (predominantly open forest to arid zone) species including the thylacomyid, *Macrotis*. This division is based on a cladistic analysis of skull characters which shows that the species within each of these two groups of bandicoots share a unique suite of derived or specialised morphological characters. Baverstock *et al.* (1990), using immunological techniques, also failed to find any evidence for placing *Macrotis* in a separate family from all other bandicoots. There appears to be a case for reuniting the peramelids and thylacomyids; the familial status of the latter, therefore, must be considered uncertain. Accordingly, where it is appropriate, reference is made to work on *Macrotis* in this chapter to indicate similarities and differences between these groups.

The first bandicoot to be described, the Southern Brown Bandicoot, was placed in the genus *Didelphis*. The first bandicoot genus, *Perameles* Geoffroy, was proposed in 1803. Other Australian genera were described by the end of the 19th Century, although use of nomenclature was rather fluid due to uncertainty about the validity of some generic names (for example, *Thylacis* versus *Isoodon*: Lidicker & Follett 1968; Mackerras & Mackerras 1960) and variation in the placement of species in genera. Generic terminology now appears to be stable for Australian species.

Placement of species in genera has varied greatly since the initial use of *Didelphis*. *Perameles* has been used as a grab-bag to include several species of *Isoodon* and a number of New Guinean species. Thomas (1888) placed the following modern species in *Perameles*: Long-nosed Bandicoot, Eastern Barred Bandicoot (*P. gunnii*), Western Barred Bandicoot, Southern Brown Bandicoot, Northern Brown Bandicoot (*I. macrourus*), two species of *Echymipera* and three species of *Peroryctes*. The more distinctive groups, *Chaeropus* and *Macrotis*, were placed into separate genera at the time of their description. Thomas (1906b) divided the Australian and Papuan bandicoots into four genera, including *Isoodon* Desmarest. Since then, the generic groupings of the Australian species have been stable. Work has continued, however, on the resolution of the New Guinean genera (Groves & Flannery 1990).

Early biologists described many species which have gradually become reduced in number as better collections accumulated and improved knowledge of natural variation in the groups became available. Australian species are still being revised. Specific problems exist in *Isoodon*, particularly the Southern Brown/Golden Bandicoot group (Close *et al.* 1990) and in the Western Barred Bandicoot group. Lyne & Mort (1981) recently proposed a new species arrangement for the Southern Brown Bandicoot group, with description of a new species, *I. arnhemensis*.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The external characteristics of bandicoots are a reflection of their adaptive role as medium-sized, cryptic insectivores.

Most bandicoots are rabbit-sized or smaller, falling within a size range of about 250–500 mm head/body length and 500–2000 g weight. Smaller sizes are seen in island races (*Isoodon obesulus nauticus*, *I. auratus barrowensis*, *Perameles bougainville bougainville*) and arid zone species (*P. bougainville*, *I. auratus*). This may be associated with a poorer or less dependable insect food supply in such localities. The extreme is shown by the Mouse Bandicoot, *Microperoryctes murina*, with a head/body length of 150–170 mm, comparable in size to that of a large dasyurid. This may be associated with high altitude (2500 m) or a presumed fossorial mole-like life (Tate & Archbold 1937). Competition with the larger dasyurids may inhibit any evolutionary trends to smaller size in Australia. Larger sizes are most common at lower latitudes, culminating in the tropical species, the Giant Bandicoot, *Peroryctes broadbenti*, with a head/body length of 390–560 mm and maximum weight of over 4700 grams. Larger body sizes may reflect life in regions with a more prolific food supply. Body size may be sexually dimorphic, such dimorphism being more pronounced in larger species, or greatly reduced or absent in smaller species (Freedman & Joffe 1967b; Freedman & Rightmire 1971). Sexual dimorphism has been associated with differing social organisation (see below).

All Australian species are darker dorsally and laterally and usually white ventrally, mostly showing a drab and more or less uniform dorso-lateral coloration which becomes lighter on the lower sides. The poor development of prominent colours or conspicuous body markings is consistent with their cryptic behaviour. Development of transverse rump bars and a faint shoulder bar, however, occurs in *Perameles*, including occasional juvenile Long-nosed Bandicoots which are nearly always of uniform coloration when adult (Lyne 1964). These bars may act as disruptive camouflage in a genus which makes more use of open habitats where it may be more conspicuous. Rufous Spiny Bandicoots exhibit pronounced antero-posterior differentiation, with the development of a blackish brown pelt on the top of the head and muzzle. Longitudinal body stripes occur in some species of *Peroryctes*, the striped bandicoots.

The coloration results from a mixture of a few basic hair colours and sometimes from a display of underfur. Overall colour is a result of variation in proportion of hairs of each colour present and variation in the tone. Basic hair colours are browns, fawns, rufescent tones and white. A wide range of all the above colours occurs in three of the four genera. Strong rufescent tones are common in the desert species, Desert and Golden Bandicoots and in the tropical Rufous Spiny Bandicoot. Grey underfur may be displayed on fore- and hind limbs. This type of coloration forms another minor distinction from the bilbies, which have another basic hair colour present, blueish or silvery grey and a different approach to colour variation - the widespread exposure of grey and white underfur dorsally and laterally.

Hairs are short and stiffish in contrast to the long silky hairs of bilbies and concavo-convex in cross section with a longitudinal groove on one side (Brunner & Coman 1974). Hairs of the Rufous Spiny Bandicoot appear stiffer and broader than others, over 0.5 mm wide, leading to its common names. Lyne (1951, 1952, 1957) described hairs and hair development in various species.

Limb morphology again reflects the bandicoot ecological role. The shortening of the forelegs relative to the hind legs and their thickset structure correlates with their function as digging tools, presumably increasing their mechanical advantage when digging. The strong flattened foreclaws serve a similar function. Lengthening of the limbs for running and reduction of digits occurs in Pig-footed Bandicoots (see above). In pouch young of this species, however, the limbs and digits are closer to the normal bandicoot condition (Krefft 1866, p. 14; Lyne 1952).

Bandicoots may show slight variation in foot structure, the significance of which is uncertain. Digit I of the hind foot is largest in Rufous Spiny Bandicoots (Tate 1948). Lyne (1951) described a difference in the relative length of digits II/III and V between Eastern Barred Bandicoots and *Perameles fasciata* and Tate (1948) described differences in relative lengths of digits in *Perameles* and *Isodon*.

Hyper-development of the tarsal pad behind digits IV and V occurs in the Dimorphic Echymipera, *Echymipera clara* (Tate, 1948).

Deciduous claws are present in newly born young to assist their journey to the pouch. The manus of the Southern Brown Bandicoot and the Eastern Barred Bandicoot has deciduous claws on digits II, III and IV which are shed soon after reaching the pouch (Lyne 1952, 1974b).

The ears are short and rounded in *Isodon* and *Echymipera*. Lengthening occurs in *Perameles* and greatest length is reached in *Chaeropus*, up to about 60 mm. More elongate ears appear to correlate with the use of more open habitats.

The pouch opens to the rear. This arrangement presents the young with the shortest route to the teats at birth, in contrast to the more hazardous situation in macropods and phalangerids. Expansion of the pouch with growth of the young occurs mainly forwards along the abdomen to the level of the forelegs. Eight nipples are usually present with six in the New Guinean species, *Echymipera kalubu* (= *E. doreyana*, see Tate 1948).

The tail is generally short and non-prehensile. The Rufous Spiny Bandicoot has a sparsely furred tail that is almost naked and about one quarter the length of head and body. Most species have a longer, closely furred tail with the body coloration dorso-laterally and white hairs ventrolaterally. A well-defined dark dorsal tail stripe occurs in Eastern Barred Bandicoots (near tail base) and Western Barred Bandicoots (full length of tail). The Pig-footed Bandicoot has the longest tail, slightly more than half the head and body length, with a short terminal crest on dorsal and ventral surfaces.

Skeletal System

Bandicoots have a typical marsupial skeleton, but exhibit some peculiarities. Peramelids are the only marsupials with a well-developed patella or knee-cap (Jones 1924). They also are the only marsupials to lack clavicles (Jones 1924). The clavicle is characteristic of mammals in which the forelimbs are capable of great freedom of movement; specialisation of the forelimb for digging in bandicoots correlates with the absence of the clavicle. The hind limbs, in contrast, show more cursorial adaptation - the femur, tibia, fibula and digits are elongate relative to the forelegs and the foot structure is unique (see below). Well-developed epipubic or marsupial bones are present.

Lengthening of the rostrum is characteristic of perameloids. It is least developed in *Isodon* and *Chaeropus* and most prominent in *Rhynchomeles* and *Echymipera*. Tate (1948) suggested that the development of lambdoidal ridges at the back of the skull is related to the bandicoots 'pig-like habits' of rooting in the soil and vegetation. Fenestration of the palate (Fig. 24.2) is present throughout the family and varies within genera (Tate 1948). It may be most pronounced in arid and semi-arid species.

The basicranial region has been considered by Archer (1976b) and Archer & Kirsch (1977). There is a tendency to increase the size of the auditory bullae (Fig 24.2) in some species occurring in semi-arid and arid areas, particularly in *Isodon*. This has been associated with predator avoidance in other groups of mammals (Archer 1981a). The simple basicranial pattern, with little development of the periotic tympanic wing and other structures, is seen in *Peroryctes*, *Microperoryctes* and most species of *Perameles*. *Isodon* and, to a

lesser extent, *Chaeropus*, depart from this pattern. *Isoodon* has an enlarged hypotympanic and epitympanic sinus, analogous to those of *Macrotis* and the basicranial structure may be used to separate 'structurally ancestral perameloids such as *Perameles* and *Peroryctes* from specialised forms such as *Isoodon*, *Chaeropus* and *Macrotis*' (Archer & Kirsch 1977).

Skull morphology and dentition have been described by various workers during taxonomic studies. Freedman (1967), Freedman & Joffe (1967a, 1967b) and Freedman & Rightmire (1971) described skull characters of *Perameles* and *Isoodon*. Characters examined include sexual dimorphism, fenestration of the palate, auditory bullae and teeth. Dixon (1978, 1981) and Lyne & Mort (1981) used cranial morphology in studying the taxonomy of *Isoodon*.

Locomotion

Perameloids have a foot structure unique among marsupials. The body weight is transferred to the hind foot via a mechanism including contact between the ectocuneiform and fourth metatarsal bones (Marshall 1972) (Fig. 24.4). This arrangement, convergent with that of the ungulate foot, is an adaptation for a cursorial life which permits body weight to be transferred to the distal tarsus. Marshall (1972) suggested that 'the ectocuneiform metatarsal four contact is the diagnostic character which truly sets peramelids apart from their contemporary relatives'.

Locomotion has not been described in detail. The breadth and elongation of the hind foot varies, presumably as a locomotory adaptation to suit their behaviour and environment. Thus, *Echymipera* possesses relatively short broad hind feet. The elongate hind foot is further attenuated in some species - *Peroryctes raffrayanus*, *Macrotis*, *Chaeropus* - leading Tate (1948) to suggest 'saltation'. There is, however, no evidence of a bipedal hopping gait in any bandicoot and the varying degree of elongation of the hind foot may instead be associated with enhancement of the bounding progression commonly seen in fast-moving bandicoots. The use of a bounding gait as a means of moving rapidly may be an evolutionary consequence of the need to retain short, powerful forelegs for digging. The longer hind legs then become the main agent of rapid locomotion and a bounding gait results. *Chaeropus*, however, also shows elongation of the foreleg. Its shift to a more herbivorous diet (see below) has apparently freed the foreleg from its prime digging function, permitting greater elongation and improved running ability. The locomotion of *Chaeropus* as described by Krefft (1866) - progressing 'like a broken-down hack in a canter, apparently dragging the hindquarters after it' - is totally different from that of other bandicoots, indicating a marked change in their adaptive mode.

Bipedal locomotion is, however, possible in some circumstances. Thus, the Northern Brown Bandicoot adopts a bipedal stance, with body held nearly vertically, during intraspecific conflict and slowly hops and walks short distances towards its opponent in this posture.

Northern Brown Bandicoots can jump vertically to heights of nearly 2 m when chased in captivity. Jones (1924) stated that Western Barred Bandicoots may make similar vertical jumps in the wild when alarmed, also stating that it is an animal of 'astonishing activity ... When fully active in the twilight its movements are more reminiscent of those of birds than those we usually associate with mammals'.

Feeding and Digestive System

Teeth are rooted, sharp, cutting and adapted to an insectivorous diet. Upper incisors have flattened crowns, are slender (laterally compressed) and subequal except in Pig-footed Bandicoots which have stout broad incisors in both upper

and lower jaws, reminiscent of those of a folivore (Fig. 24.2). Canines are slender and pointed. The latter are sexually dimorphic in some species, being larger in males (for example Northern Brown Bandicoots, Lyne & Mort 1981) (Fig. 24.2). Premolars are narrow, with a simple point and molars either quadrate or triangular and multicuspid (Thomas 1888). Molar shape has been used as a taxonomic character in *Echymipera* and other groups, quadrate molars being considered more specialised (Tate 1948; Van der Feen 1962). The deciduous premolar (or molar) is present, being replaced by the posteriormost permanent premolar. Archer (1976a) described the morphology of molar cusps and contrasts them to those of dasyurids and didelphids.

Archer (1976a), Archer & Kirsch (1977), Bensley (1903) and Rich (1982) discussed upper molar morphology and evolution (see above). Freedman (1967), Freedman & Joffe (1967a, 1967b) and Freedman & Rightmire (1971) described teeth and teeth dimensions in *Perameles* and *Isoodon*. Kingsmill (1962) showed age of tooth eruption in Long-nosed Bandicoots. Lyne & Mort (1981) showed age of tooth eruption in Northern Brown Bandicoots and described pathological tooth loss in that species in captivity. Development of the teeth of pouch young was described by Fosse & Risnes (1972a, 1972b). Abnormal dental development in peramelids was reviewed by Archer (1975) and Miller (1977) reported on tooth loss in Northern Brown Bandicoots due to disease.

Bandicoots are omnivorous and all possess a caecum. The caecum is most elaborate in *Macrotis*, decreases in complexity in *Perameles* and *Isoodon* and is extremely simple and generalised in *Echymipera* (Hill & Rewell, 1954). The caecum of *Chaeropus* is relatively longer than that of *Perameles* 'suggesting that plant material probably constituted a significant part of this animal's diet' (Hume 1982; Parsons 1903). The premolar morphology of *Chaeropus* (see above) is also consistent with this observation and its intestinal length is also relatively greater (Tedman 1990). Tedman reviews other aspects of anatomy of the digestive system. The spleen of Northern Brown Bandicoots is much larger than that of *Perameles* spp. and spleen morphology seems to be variable.

The rate of passage of food (termites) in bandicoots is fast compared to that found in other similar-sized marsupials (Griffiths 1968). The activity of enzymes like trehalase, which may be related to the insect component of their diet, is extremely high in some peramelids (Kerry 1969). According to Jones (1924), bandicoots regurgitate their food after a meal and reingest it.

Food appears to be detected by smell, either from below the ground, from the ground surface or from low vegetation. Peramelids gather much of their food by digging in the soil with their forelegs, producing either simple scratchings or characteristic, pointed, conical holes.

Metabolism and Temperature Regulation

The standard metabolism of all peramelids studied, unlike *Macrotis* species, is the same as that for other marsupials (Hulbert & Dawson 1974a). Bilbies have a metabolism that is further reduced compared to the already low level of metabolism in marsupials and it has been suggested that this is an adaptation to the energetic constraints of its arid environment (Hulbert & Dawson 1974a). All bandicoots examined are competent homeotherms in the cold. They are capable of elevating their metabolism up to four-fold by shivering, in order to maintain a constant body temperature in the range of 34-36°C. Fur insulation is similar in tropical, temperate and desert species. Northern Brown, Eastern Barred and Rufous Spiny Bandicoots show seasonal changes in fur insulation (Hulbert & Dawson 1974b).

In the heat, Long-nosed and Northern Brown Bandicoots are able to maintain sublethal body temperatures by panting and the licking of saliva on their body surface. *Isodon* species are more capable of withstanding heat stress and can evaporate 40% of water loss via panting, 40% via salivation and licking whilst the remaining 20% is via insensible cutaneous evaporation (Hulbert & Dawson 1974b). This contrasts with temperature regulation in the desert thylacomyid, the Bilby, which shows no evaporative responses to heat stress and is unable to cope with high environmental temperatures (Hulbert & Dawson 1974b). It is thus extremely dependent on the micro-environment of its burrow and would probably die if exposed on a hot summer's day. It probably also has limited capacity to cope with the heat generated by exercise and if chased for any period of time would also probably die from hyperthermia. This may have been a factor in its local extinction in many areas of Australia.

Excretion

All peramelids examined are capable of producing a reasonably concentrated urine and, in correlation with their low metabolic rate, they have a low water turnover (Hulbert & Dawson 1974c). This is partly due to the fact that peramelids are able to reduce their respiratory water loss by a nasal counter current mechanism similar to that observed in many small rodents. The long nose may be an advantage in this respect, allowing it to conserve large amounts of water (Hulbert & Dawson 1974b).

A study of water turnover in a free-living population of Northern Brown Bandicoots indicates that there is little seasonal variation in water metabolism. When free surface water was available, however, the bandicoots drank it and had a water turnover much greater than that measured in the laboratory (Fig. 24.6) (Hulbert & Gordon 1972). This study also indicated, however, that *Isodon* does not require free surface water and is able to maintain water balance without it. Lactation results in an increased water turnover both in the wild and in the laboratory (Hulbert & Dawson 1974c; Hulbert & Gordon 1972).

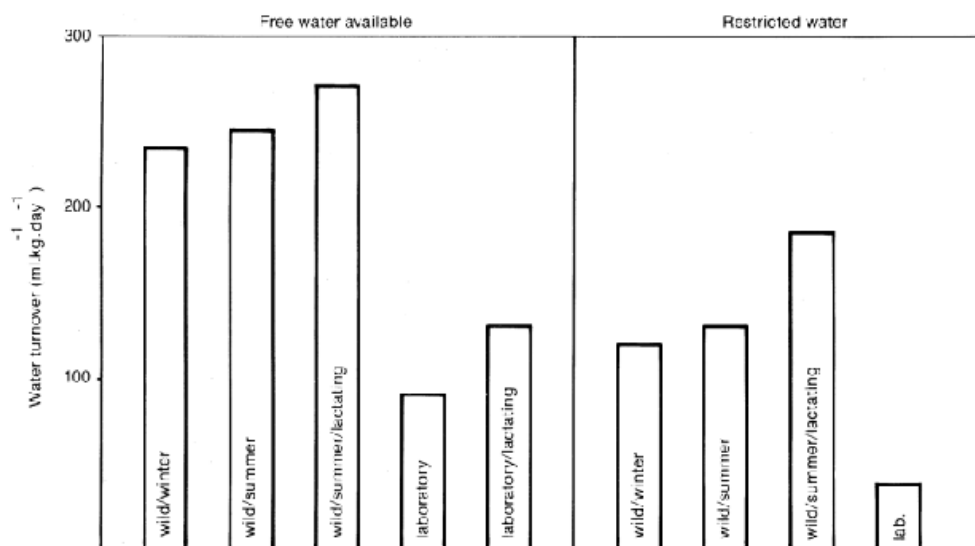


Figure 24.6 Water requirement of the bandicoot Northern Brown Bandicoot under different conditions. (Data from Hulbert & Gordon, 1972; Hulbert & Dawson, 1974c)

Burger & Cross (1982) described kidney microanatomy in Northern Brown Bandicoots and Tedman (1990) described gross anatomy of the urogenital system.

Endocrine and Exocrine Systems

Green (1963a) described skin glands in Northern Brown Bandicoots and Tedman (1990) described glands of the digestive tract of Northern Brown Bandicoots including rectal, submaxillary and sublingual glands. Peramelids possess a thoracic thymus gland, but no cervical thymus (Tedman 1990).

Little is known of endocrine systems, although some work has been carried out on thyroid function and the function of the corpus luteum. The thyroid gland in the Long-nosed and Northern Brown Bandicoots shows active hormone secretion and the plasma concentration of both thyroxine and triiodothyronine is similar in Northern Brown Bandicoots to the level found in other marsupials. Thyroidectomy in this species results in a significant decrease in resting metabolic rate (Hulbert & Augee 1982a).

The corpora lutea of pregnancy persist during lactation, a unique condition within the Metatheria (Gemmell 1981). The concentrations of progesterone in the plasma of lactating female Northern Brown Bandicoots correlate with the presence of granules in the luteal cells that are thought to contain progesterone and relaxin (Gemmell 1979). Progesterone concentration in the plasma increases to a plateau which is maintained into early lactation. The elevated plasma concentration probably arises from the corpora lutea. The corpora lutea cease secretion in the middle stages of lactation (Gemmell 1981), although morphological change is slight until the end of lactation (Gemmell 1981; Hollis & Lyne 1980; Lyne & Hollis 1979). Early in lactation, when secreting progesterone, the corpus luteum is thought to inhibit ovulation (Gemmell 1981). Birth in Northern Brown Bandicoots has been correlated with increased levels of prostaglandins (Gemmell, Jenkin & Thorburn 1980).

Castration of Northern Brown Bandicoots results in a decline in testosterone levels in the plasma and partial involution of the prostate gland (Macdonald & Hughes 1977). Concentration of plasma testosterone fluctuates seasonally, peaking in the breeding season (McFarlane *et al.* 1990).

Reproduction

The chromosome number is $2n = 14$. One sex chromosome, an X in females and the Y of males, is eliminated from most somatic tissues during development. Rates of sex chromosome loss vary between individuals and between particular tissues (Close 1984). Ullman (1979) describes the ultrastructure of oocytes and Sapsford *et al.* (1969a) described the maturation of spermatids.

A short urogenital sinus joins two long straight lateral vaginae, which terminate anteriorly in expanded portions, the vaginal caeca or seminal receptacles (Hill 1899; Lyne & Hollis 1982) (Fig. 24.7). The vaginal cul-de-sac connects these structures to the uteri, the fallopian tubes and the ovaries. Bandicoots differ from other marsupials in the forward position of the bladder, the long urethra, expanded vaginal caeca, small vaginal cul-de-sac and short urogenital sinus (Tedman 1990).

As in many other marsupials, young are born via a temporary birth canal which forms between the lateral vaginae, running from the vaginal cul-de-sac to the urogenital sinus (Hill 1899; Lyne & Hollis 1982).

Long-nosed and Northern Brown Bandicoots have the shortest gestation period recorded for any mammal, approximately 12.5 days in both species (Hughes 1962b; Lyne 1974b). *Isoodon* and *Perameles* are polyoestrous and in Long-

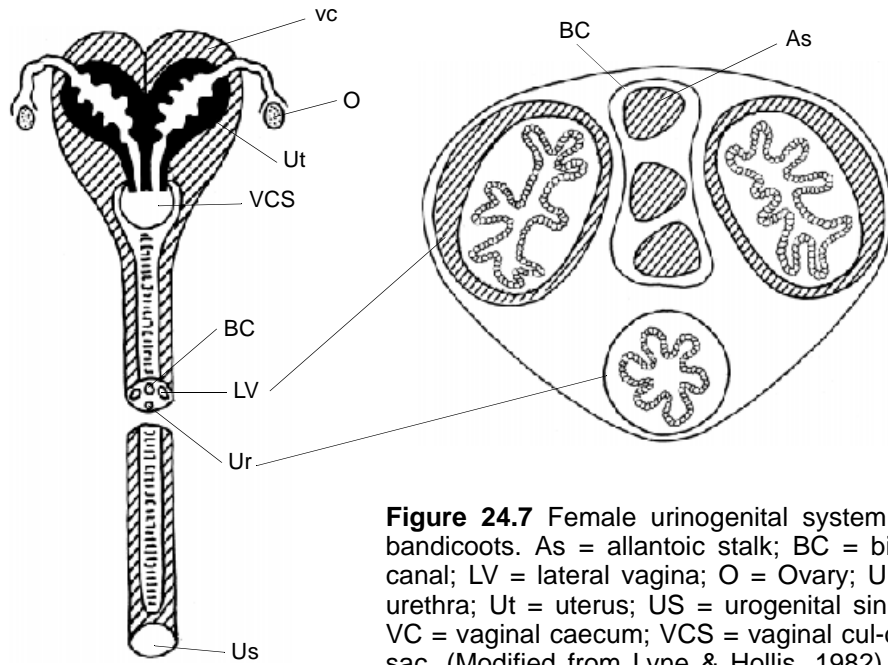


Figure 24.7 Female urinogenital system of bandicoots. As = allantoic stalk; BC = birth canal; LV = lateral vagina; O = Ovary; Ur = urethra; Ut = uterus; US = urogenital sinus; VC = vaginal caecum; VCS = vaginal cul-de-sac. (Modified from Lyne & Hollis, 1982) (© ABRS) [B. Scott]

nosed Bandicoots the oestrus cycle is variously recorded as about 26 days (Hughes 1962b) or about 21 days (Lyne 1976). In Northern Brown Bandicoots it is about 20 days (Lyne 1976).

Suckling suppresses oestrus during most of the pouch life except during the terminal period, when a 'lactation oestrus' occurs and the female may be fertilised again so that the existing litter can be replaced by a new litter at the time of weaning (Close 1977; Gordon 1971, 1974, 1984; Lyne 1964; Stodart 1977). Litters may then be replaced continuously during an extended breeding season.

Female body weight increases during lactation to mid-lactation, then decreases. The weight increase is apparently an adaptation to enable the female to meet the demands of the young for milk (Gordon 1971; Merchant 1990). The latter author suggests that it is under hormonal control and stimulated by suckling.

Peramelids reach sexual maturity at a very early age. Gordon (1971) records that female Northern Brown Bandicoots, as young as 96 days, give birth to young in the same breeding season as they themselves are born. This early sexual maturation, rapid growth and fast rate of reproduction led Sharman (1965) to express the opinion that in many ways, the peramelids parallel the rodents. They have become uniquely specialised among marsupials for a high reproductive rate and reduced maternal care.

Mating occurs at night and consists of a period of following by the male, brief mounting and copulation. This is followed by a waning of attraction (Stodart 1966a).

Breeding may be seasonal or non-seasonal (Gemmell 1982; Gordon 1971, 1974; Hall 1983b; Heinsohn 1966; Stoddart & Braithwaite 1979). The mechanisms controlling breeding are not established and various factors have been suggested as controlling agents. In at least some populations of Northern Brown Bandicoots, food availability has been correlated with onset of the breeding season (Friend 1990; Gordon 1971). Barnes & Gemmell (1984), however, found a correlation between proportion of lactating females and rate of change of minimum temperature in four different regions.

Stoddart & Braithwaite (1979) suggest that photoperiod initiates breeding in Southern Brown Bandicoots. Heinsohn (1966) also postulates initiation of breeding by photoperiod and termination due to food availability in Eastern Barred Bandicoots.

Tedman (1990) reviewed male accessory glands and the male reproductive system, which are generally similar to that of other marsupials.

Embryology and Development

In Northern Brown and Long-nosed Bandicoots, early embryos are of similar size to unfertilised ova and expansion in size does not occur before the 75-cell stage of development. Subsequently, the number of cells increases considerably from the late unilaminar blastocyst. Egg membranes (zona pellucida, mucoid coat, shell membrane) are similar to those of other marsupials. The rate of embryonic development appears to be similar to that of the Virginia Opossum, *Didelphis virginiana*, which has a rather similar gestation period (Lyne & Hollis 1976).

As in some other marsupials, Seessel's pouch in Northern Brown Bandicoot is involved in the formation of the anterior pituitary (Hall & Hughes 1985). Organ development at birth is only sufficient to initiate and maintain early pouch life and morphological development of the anterior pituitary is less advanced than in eutherians with short gestation periods (Hall & Hughes 1985).

One of the most significant features of reproduction in peramelids is the presence of a functional chorioallantoic placenta (Fig. 24.8), in addition to the yolk-sac. The former has evolved independently of the placenta found in eutherians (Hill 1897; Hughes *et al.* 1990; Padykula & Taylor 1976, 1977; Sharman 1965) and is probably functionally correlated with the rapid rate of development in peramelids. Towards the end of gestation, the chorioallantoic placenta supersedes the yolk-sac as the major extraembryonic organ for respiration and metabolic exchange (Hughes 1984).

The young of *Perameles* and *Isodon* are born relatively large and advanced and undergo the most rapid growth and development of all marsupials (Lyne 1964; MacKerras & Smith 1960). Peramelid young are born at twice the weight of *Didelphis* young and have taste buds, partially formed Müllerian ducts and partially formed ear pinnae, all absent from *Didelphis* (Padykula & Taylor, 1977). Subsequent development of young is described by Hall (1990), Kingsmill (1962), Lyne (1951, 1952, 1964) and MacKerras & Smith (1960). In Northern Brown Bandicoots, digits and claws of the hind feet do not appear until about 7 days age, whereas front feet digits are separate and clawed at birth, for use in crawling to the pouch (Hall 1990). The pouch is visible at 7 days, scrotum at 9 days, mystacial vibrissae at day 18 and a fine cover of body hair at day 40, while the eyes begin to open at about day 45 (Hall 1990). Milk consumption by the young is relatively greater than in some other marsupials and milk is also more concentrated (Merchant 1990). Milk composition changes during lactation, lipid concentration increasing and carbohydrates decreasing. Composition then changes again, rapidly, in late lactation to support the next litter (Merchant 1990).

Development of the pituitary-thyroid axis and thermoregulation has been examined in Northern Brown Bandicoots. Hall & Hughes (1985) report that thyrotrophs are the first cell types to appear in the anterior pituitary and are present in seven day old pouch young. Although a presumptive thyroid gland is present in new-born Northern Brown Bandicoots, the first signs of thyroid hormone secretion are not seen until day 30 and a maximum activity is present around day 50 (Johnston & Gemmell 1987). This peak in thyroid activity is correlated with the development of both hair and thermoregulatory capacity during the last two weeks of pouch life (Gemmell & Johnston 1985).

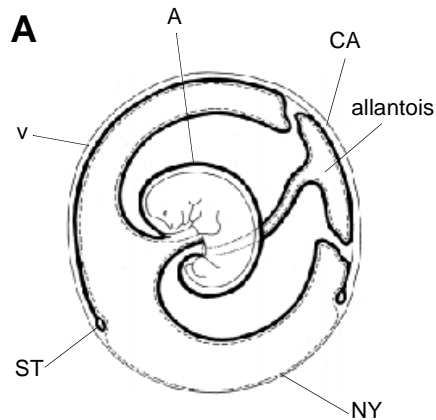
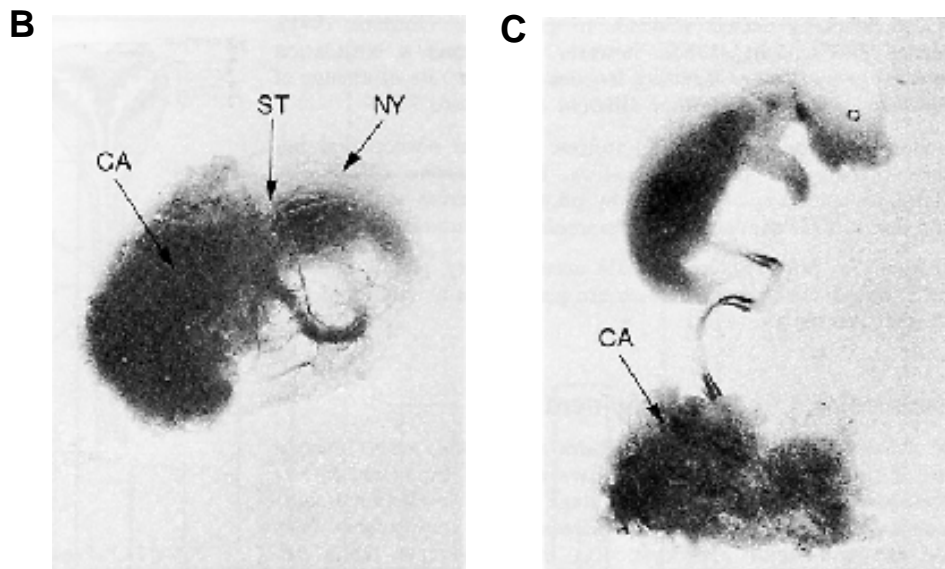


Figure 24.8 **A**, Bandicoot embryo showing chorio-allantoic placenta and yolk-sac placenta. (Modified from Padykula & Taylor, 1976); **B**, full term fetus of Long-nosed Bandicoot within fetal membranes; **C**, dissection of the fetus shown in **B**. An umbilical cord connects the fetus with the chorio-allantoic placenta. A = amnion, CA = chorio-allantoic placenta, NY = non-vascular yolk sac placenta, ST = sinus terminalis, V = vascular yolk sac placenta. (© photos R.L. Hughes) (a, © ABRS) [B. Scott]



Northern Brown Bandicoot populations in New South Wales show seasonal influences on adult growth, with high rates of weight increase in winter to early spring each year, followed by relatively stable weights through spring and summer (Gordon 1971). This growth pattern suggests that size increase is influenced by a seasonal growth rhythm, a mechanism that would prepare the animal for the coming breeding season.

NATURAL HISTORY

Life History

Life history characteristics are typical of those of '*r*-selected' mammals. This kind of life history is particularly important for species which live in low ground cover, an unstable habitat, subject to frequent and unpredictable destruction by fire, drought, or grazing animals. There have even been suggestions that some peramelids are adapted to take advantage of the benefits arising from habitat destruction in the form of the increased insect food supply that may be present in regenerating vegetation. Life in an unstable habitat thus has both an adverse and a favourable aspect. While there may be future uncertainty and the possibility of some unpredictable disaster, this may entail the creation of new opportunities that may be rapidly exploited by species with sufficient ecological flexibility.

Little is known of longevity. Northern Brown Bandicoots in New South Wales can live until at least three years of age (Gordon 1971) and Eastern Barred Bandicoots reach at least 3 years in captivity (Heinsohn 1966).

Where population dynamics have been studied, population size has ranged from being relatively stable to quite the reverse. This correlates with the broad habitat tolerance of many bandicoots and their ability to exploit rapidly even marginal situations that may become temporarily suitable for them. A population of Eastern Barred Bandicoots in Tasmania had dropped to one third of its initial level by the end of one study (Heinsohn 1966) and a population of Northern Brown Bandicoots in the Northern Territory became extinct in the study area (Friend 1990). Populations may also show marked seasonal effects on characteristics such as numbers, reproductive rate and condition of animals.

An island population of Northern Brown Bandicoots in New South Wales showed regular annual peaks in population size due to the annual influx of new young. These peaks were absent from a mainland population, as most young there were able to disperse from the area before becoming trappable (Gordon 1971). Friend (1990) found two annual peaks in Northern Brown Bandicoots in the Northern Territory, the first in February, due to recruitment of juveniles into the population, the second in September/October, due to an increase in the number of males in the early breeding season. Populations of Southern Brown Bandicoots in Victoria and Tasmania and Eastern Barred Bandicoots in Tasmania lack annual fluctuations (Heinsohn 1966; Stoddart & Braithwaite 1979). Stoddart & Braithwaite (1979) showed that older and larger Southern Brown Bandicoot males dominate the use of optimal habitat.

Litter size ranges from one to seven in Northern Brown Bandicoots, but usually lies in the range of one to four young with a mean size of about three young. Mean litter size may vary between seasons and within each breeding season in Eastern Barred Bandicoots (Heinsohn 1966), Northern Brown Bandicoots (Friend 1990; Gordon 1971) and Southern Brown Bandicoots (Stoddart & Braithwaite 1979). Some studies have correlated mean litter size with maternal body weight and others have failed to find any such relationship (Friend 1990). Merchant (1990), however, found a correlation between mean litter size and the magnitude of maternal weight gain during lactation. Litter size may therefore be tied to a maternal response to seasonal conditions. Stoddart & Braithwaite (*op. cit.*) hypothesise that the variation in mean litter size is an adaptive response to population characteristics, arguing that the Southern Brown Bandicoot oscillates about a semelparity/iteroparity continuum. More young should be produced in situations of high or variable juvenile mortality combined with low adult mortality and *vice versa*. Friend (1990) suggests that variable reproductive rates (resulting from mean litter size, length of breeding season, incidence of breeding) in Northern Brown Bandicoots are a response to environmental conditions, with breeding intensity being increased in the more highly seasonal areas which have short favourable periods.

Despite their high reproductive rates, bandicoots do not have an especially large litter size, particularly if they are compared to some eutherians, such as certain rodents. This may reflect an inherent limitation for many marsupials, in that large litters are constrained by the need to be able to carry all of the young in the pouch. Marsupials with very large litters are the dasyurids and didelphids, which either do not have this constraint, or have older young that are carried clinging to the mother's body. Peramelids have had to develop adaptations other than very large litter size to attain their high reproductive rates.

Length of the breeding season varies regionally in Northern Brown Bandicoots and possibly others (Barnes & Gemmell 1984; Friend 1990; Gordon 1971) ranging from 12 months near Brisbane to periods of 6 months or more in other areas. This is likely a response to some aspect of environmental seasonality that

may vary from area to area (Friend 1990). In the less seasonal situations with longer breeding seasons, incidence of breeding appears to be lower or more variable (*e.g.* Hall 1983b), whereas it is maximised in the highly seasonal situations 'to take advantage of the shorter breeding period' (Friend 1990).

Young Northern Brown Bandicoots leave the pouch at about 50 days and are weaned by about 60 days of age, a very rapid rate of development. By way of comparison, in Common Ring-tail Possums, *Pseudocheirus peregrinus* (a similarly-sized marsupial), young leave the pouch at about 4 months age and wean at about 6 months. In peramelids, both pouch development and subsequent maternal care is therefore much compressed. The rapid development of young enables the females to produce a successive litter quickly (see above); litter production may attain a rate of one litter every 2 months in favourable conditions. In this way, high reproductive rates are attainable.

Survival in Northern Brown Bandicoots is characterised by loss of young during pouch life (at least in some populations, Gordon 1971, but see Hall 1983b) and heavy loss of weaned young prior to maturity (Fig. 9). Other species (for example, Southern Brown Bandicoot, and Eastern Barred Bandicoot (Stoddart & Braithwaite 1979; Heinsohn 1966) exhibit similar patterns of survival. Rate of dispersal of young from the natal area also appears to be high and rapid; few manage to establish there (Friend 1990; Gordon 1971, 1974).

Age of maturity is variable, apparently in response to environmental conditions. Female Northern Brown Bandicoots may first breed at ages ranging from 96 to about 200 days (Gordon 1971).

Three male Northern Brown Bandicoots commenced sperm production at approximate ages of 200, 200 and 300 days (Gordon 1971). Such early maturity enables animals to reproduce in the breeding season of their birth.

Population studies have recorded high rates of transience (Fig. 24.9). Individuals appear well able to move to escape from unfavourable situations or exploit new opportunities in regenerating habitat. This correlates with the high reproductive rate and low recruitment rate as a component of adaptation to an unstable habitat (Friend 1990; Gordon 1971; Stoddart & Braithwaite 1979).

The basic pattern of birth, high juvenile mortality and high rates of dispersal, maturity, establishment in a home range and lower adult mortality is subject to much variation due to population pressures and extrinsic factors, such as habitat

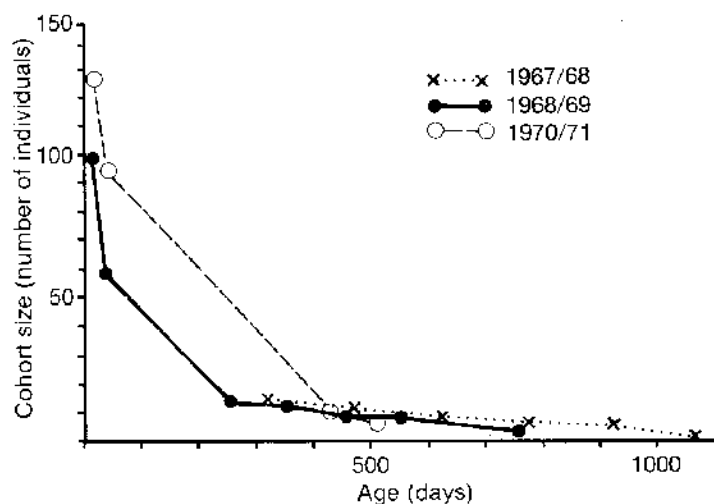


Figure 24.9 Survival in the population of annual cohorts of Northern Brown Bandicoots at Smiths Lake, New South Wales (Gordon 1971). Loss of animals from the population is due to a combination of dispersal and mortality.

change. Establishment in a home range is difficult and tenure of home ranges may be short. Reproductive rates are variable in different situations for reasons that are not clearly understood.

Ecology

So far as is known, peramelids are ecologically flexible, consistent with their other *r*-selected characteristics. They are among the few Australian mammals to be found commonly among the urban fauna of Australian towns and cities.

The diet is opportunistic and omnivorous, with an apparent preference for invertebrates (Dixon 1985; Harrison 1962a; Heinsohn 1966; Jones 1924; Krefft 1866; McKeown 1951; Sandars 1952; Stoddart & Braithwaite 1979; Watts 1974c). Southern Brown Bandicoots at a heathland site in Victoria included the subterranean fruiting bodies of hypogeous sporocarpic fungi in the diet (Lee & Cockburn 1985). The Pig-footed Bandicoot is thought to have had a more herbivorous diet (see above). Krefft (1866) fed his animals on 'lettuces, barley grass, bread and some bulbous roots'. They would not eat meat or mice and the dung of wild animals was entirely composed of grass. This exceptional bandicoot may have been primarily a herbivore or even a folivore.

Habitat preference has been related to vegetation structure. The two sympatric Tasmanian peramelids show contrasting habitat utilisation. Southern Brown Bandicoots prefer areas with low ground cover, scrub and heath and the Eastern Barred Bandicoot forages in these areas as well as open paddocks (Heinsohn 1966). In Brisbane and central coastal New South Wales, the Northern Brown Bandicoot occurs in areas of close ground cover (Gordon 1971, 1974). In the Northern Territory, the Northern Brown Bandicoot is strongly associated with specific vegetation structure and floristics, occurring in layered open forest during the dry season (Friend & Taylor 1985). This relationship dissolves during the wet season, possibly because the food resource is then more widespread and abundant. At a site in Victoria, the Southern Brown Bandicoot has a preference for regenerating heath (Braithwaite & Gullan 1978; Stoddart & Braithwaite 1979). A rather similar situation occurs in Tasmania, where Southern Brown Bandicoots are associated with recently burnt scrub and heath (Heinsohn 1966; cited in Stoddart & Braithwaite 1979). This preference correlates with the higher productivity (insect food supply) of this habitat.

At Innisfail, north Queensland, the Northern Brown Bandicoot avoids rainforest, but occurs in many disturbed areas (farmland, urban land, woodland) whereas Long-nosed Bandicoot occurs in these habitats and rainforest (Harrison 1962b).

Although bandicoot species frequently appear to have a preferred habitat with which they are primarily associated, many of the studies cited above show that they are sufficiently flexible to make widespread use of alternative habitats. A similar situation occurs with respect to the 'rainforest' fauna of New Guinea, where species of *Echymipera* and *Peroryctes* are common in grasslands (Ziegler 1977).

Dispersal of young and other subordinate animals has been attributed to intraspecific competition in Northern Brown, Southern Brown and Eastern Barred Bandicoots (Friend 1990; Gordon 1971; Heinsohn 1966). Stoddart & Braithwaite (1979) suggest that competition between adult males and females in Southern Brown Bandicoots excludes older females from optimal habitat.

Little is known of interspecific competition. Heinsohn (1966) found no clear evidence of it in his study of sympatric groups of Southern Brown and Eastern Barred Bandicoots, which had similar diets. There were differences in habitat utilisation, however and the possibility remains that this resulted partly from competitive interaction. There are indications of competitive interaction in other situations. The Eastern Barred Bandicoot, for example, shows a wider habitat

range in Tasmania, where the Long-nosed Bandicoot is absent, than on the Australian mainland (Heinsohn 1966). Similarly, the habitat range of Long-nosed Bandicoots appears to expand south of the Hawkesbury River on the New South Wales coast where the Northern Brown Bandicoot is absent, compared with a much narrower habitat utilisation to the north of the river.

Bandicoot fleas (Dunnet & Mardon 1974) and ticks (Roberts 1970) are all widespread species, usually with little host specificity to particular peramelid species. These parasites are common and east coast bandicoots are an important host in the life cycle of the paralysis tick *Ixodes holocyclus*. *Parastyvalius novaeguineae* occurs on Rufous Spiny Bandicoots in both Australia and New Guinea and is one of the few indigenous fleas shared by both landmasses. Mites and lice have also been recorded (Mackerras, Mackerras & Sandars 1953). The wide range of endoparasites recorded from bandicoots includes Protozoa, Trematoda, Cestoda, Nematoda, Acanthocephala and Pentastomida (Mackerras 1958; Mackerras *et al.* 1953). Among Australian marsupials, acanthocephalans (*Moniliformis semoni*) have only been found in peramelids.

No systematic study of the effect of predation on peramelids has been carried out. Miscellaneous records and studies of particular predators show that bandicoots are utilised by a wide range of predators (Gordon 1971; Heinsohn 1966; Menzies 1972; Robertshaw & Harden 1985; Triggs, Brunner & Cullen 1984). Road kills are a common cause of mortality for Long-nosed, Eastern Barred, Northern Brown and Southern Brown Bandicoots (see Heinsohn 1966) in districts with high traffic density.

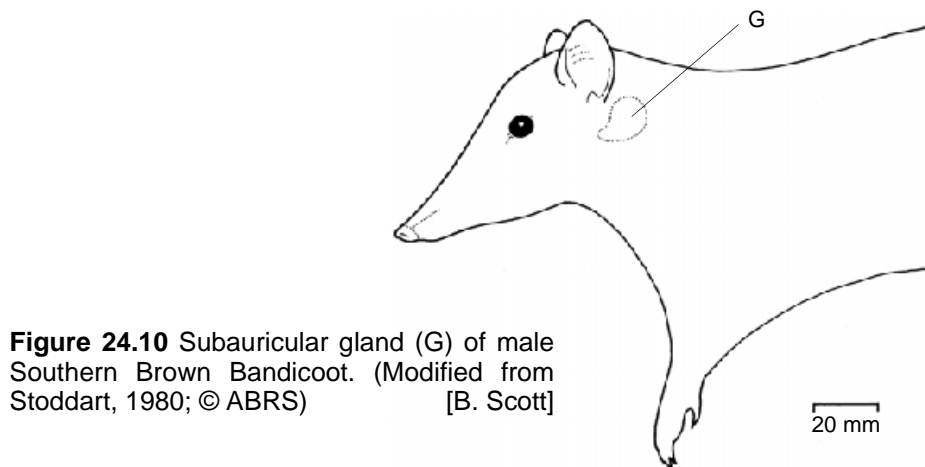


Figure 24.10 Subauricular gland (G) of male Southern Brown Bandicoot. (Modified from Stoddart, 1980; © ABRS) [B. Scott]

Social organisation is poorly known. Sexual dimorphism in body size is a key factor, at least in the larger species. The Northern Brown Bandicoot is solitary, individuals coming together only to mate. There is no lasting attachment between mother and young, contact being lost at weaning or soon after (Gordon 1974). Dominance between males is related to body size and is established by chases or fights. Opponents approach each other standing upright. The large claw on the hind foot is commonly used in aggression, one animal hopping over the other and attempting to claw the opponent with the hind foot (Gordon 1984). A scent gland occurring behind the ear (Fig. 24.10) (Stoddart 1980) in both sexes of many species is used by Northern Brown Bandicoots to mark the ground during aggressive encounters (Gordon 1984). Males are larger than females, have larger canine teeth and more extensive home ranges (for example, males 1.7–5.2 ha; females 0.9–2.1 ha) (Gordon 1974). Males carry out a rapid patrolling movement around their range each night, in addition to foraging, which apparently serves to detect intruders. Day *et al.* (1974) suggest that faeces are used as territorial markers. A free-living population of Northern Brown

Bandicoots showed a negative correlation between mean time active per night and population density, suggesting that animals avoid each other at higher densities (Gordon 1974). In the same study, Northern Brown Bandicoots occurred in overlapping home ranges with core areas which tended to be separate. A very dense island population of Southern Brown Bandicoots (8 to 11 individuals ha⁻¹) also appeared to have great range overlap (Watts 1974c). The Southern Brown Bandicoot in Victoria exhibits a complex organisation by social dominance, with optimal habitat occupied by larger dominant males and smaller animals which are tolerated there. Animals of intermediate social status are restricted to suboptimal habitat (Stoddart & Braithwaite 1979). A marked difference in home range size between males and females (63.4 acres vs 5.4 acres, respectively; Heinsohn 1966) has been demonstrated in a population of Eastern Barred Bandicoots in Tasmania, in strong contrast to Southern Brown Bandicoots in the same area.

Behaviour

Behaviour patterns of Long-nosed Bandicoots, including feeding, nest-building, grooming, reproduction and care of young are described by Stodart (1966a). Little other behavioural work has been done (see below), other than observations of wild populations.

The only known loud vocalisations occur in Long-nosed Bandicoots, which occasionally give a sharp squeaky alarm call. The Northern Brown Bandicoot emits a faint sibilant sound when threatening. The syndactylous hind feet, incisors and tongue are used in grooming (Stodart 1966a).

Female Northern Brown Bandicoots give birth lying on the side with one hind leg raised, while licking the urogenital region (Lyne 1974b). In this study, two young were born 2 minutes apart and crawled immediately to the pouch, connected by allantoic stalks to the mother. They were unaided by the mother and used the deciduous claws on the forefeet to pull themselves forwards. The mother licked around the young as they moved. The allantoic stalks appear to function as a safety cord in case the young become dislodged during the hazardous journey. Birth occurs during the day in the nest.

Female Long-nosed Bandicoots carry the young in the pouch for 50—54 days and then leave them in the nest at night while out foraging (Stodart 1966a). At day 62 or 63 the young in a captive colony followed their mother for a period, foraging with her. In wild Northern Brown Bandicoots, the period of following (young-at-foot) is either brief or non-existent (Gordon 1974). Maternal care after weaning is generally thought to be minimal.

The Northern Brown Bandicoot commences activity around dusk and this continues through most of the night (Gordon 1974). Time of cessation of activity is highly variable. The Southern Brown Bandicoot, at least, also is capable of being highly diurnal in some situations, perhaps related to food supply (Braithwaite 1977). Movement patterns of foraging Northern Brown Bandicoots show slow, onward underrated movement with little evidence of rigid patterns, such as use of fixed runways or orientation about fixed goals (Gordon 1974). Caged Long-nosed Bandicoots show intermittent activity, with alternating periods of foraging and resting in the nest (Stodart 1966a), in contrast to the continuous activity of wild animals. Activity rhythms of some captive Northern Brown and Long-nosed Bandicoot individuals demonstrate unstable synchronisation to the light-dark cycle when held under reversed daylight (Lyne 1981). The activity rhythm starts later each day.

The Northern Brown Bandicoot exhibits a relatively low level of response to novel objects (Russell & Pearce 1971) and females are significantly more active than males in open field behaviour tests (Day *et al.* 1974). Individuals trained in discrimination reversal tasks learn spatial habit reversals, but show inferior performance of visual discrimination problems (Buchmann & Grecian 1974).

Bandicoots live in nests consisting of a mass of ground litter raked together, with a chamber and a loose area in each end of the heap for entry and exit (Dahl 1897; Spencer 1897; Whittell 1954; Heinsohn 1966; Stodart 1966a; Jones 1924; Gordon 1974; Dixon & Huxley 1985). The nest is situated either in a deep depression, the surface flush with ground level (when sited on open ground) or in a shallow depression with the litter raised a few inches above the surface in a low mound (when placed in low ground cover). Bandicoots occasionally are found resting in hollow logs, under stones or under grass tussocks (Calaby 1966; Dahl 1897; Krefft 1866). Northern Brown Bandicoots abandon nests once disturbed in them (Gordon 1974).

Economic Significance

Bandicoots in suburban areas occasionally annoy householders by digging for food in lawns. Control is best effected by eradicating the lawn insects with pesticides, rather than by continually attempting remove the bandicoots.

Australian peramelids have suffered one of the greatest declines of all marsupial groups. All species of semi-arid and arid zones have either become extinct or been reduced to a few remnant populations (Frith 1973; Morton & Baynes 1985). It is known that at least some arid and semi-arid species were once relatively common. Western Barred and Southern Brown Bandicoots were common on the upper Murray River in the 1850s (Krefft 1866) and Krefft implies also that Pig-footed Bandicoots and Bilbies, at that time relatively rare on the Murray, had declined from a formerly higher status. All of these species are now extinct there. The Golden Bandicoot was 'numerous' near Broome in 1895/1896 (Dahl 1897) and 'plentiful' at Tennant Creek in the 1890s (Spencer 1897). Finlayson (1961) believed it to be formerly very widely distributed in central Australia 'wherever sandy spinifex tracts occurred in considerable expanse' and still common in the arid western parts of the Northern Territory. It is extinct or very rare in all these areas now. According to Finlayson (1961), the Desert Bandicoot was 'fairly plentiful' in 1932-1935 in the south-western corner of the Northern Territory and in the adjacent regions of South Australia and Western Australia. In Victoria, the Eastern Barred Bandicoot was common in the early 20th Century in regions where it is now extinct (Seebeck 1979) and John Gilbert implies that *Chaeropus* was common on his last expedition to the interior at unspecified localities (Whittell 1954). An important cause of population extinctions may be grazing by cattle, sheep or rabbits and the consequent change to the ground cover (Frith 1973). Alternatively, the extinctions have been blamed variously on introduced predators (foxes and cats), compaction of the soil by hooved ruminants and alteration of burning patterns (Morton & Baynes 1985; Seebeck 1979).

The Eastern Barred Bandicoot, although common in Tasmania, is highly endangered on the mainland, where the remaining colony is subject to a conservation program (Seebeck 1979). The only known surviving populations of Western Barred Bandicoots occur on Bernier and Dorre Islands off the coast of Western Australia. Islands also are important to the conservation of Golden Bandicoots, which have become extinct in most of the remainder of its range. The Pig-footed and Desert Bandicoots are thought to be extinct, as is the eastern form of the Western Barred Bandicoot with three prominent rump bars (*P. b. fasciata*).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Perameloids are one of the most wide-ranging marsupial groups of the Australian region. They occur throughout mainland Australia and Tasmania and on many of the numerous islands off the Australian coast. Farther north, they occur throughout New Guinea and on a number of nearby islands, including those of the Bismarck Archipelago to the north-east of New Guinea, the Kei and Aru Islands to the south-west and Ceram and Misool Islands to the west.

Within this broad region, a number of distribution patterns and general controlling factors can be recognised. The New Guinea region contains a group of largely endemic, forest-adapted bandicoots, the genera *Peroryctes*, *Echymipera*, *Rhynchomeles* and *Microperoryctes*. These are primarily associated with rainforests. Only one species, the Rufous Spiny Bandicoot, is shared with Australia. Their biogeography is discussed in more detail by Ziegler (1977).

On the Australian continent, a group of semi-arid zone species and a second group of coastal/subcoastal species occupying the humid zone and parts of the semi-arid zone, can be distinguished (Fig. 24.11). The former includes the Northern Brown, Western Barred, Desert, and Pig-footed Bandicoots and the thylacomyids. The second group includes the Long-nosed, Eastern Barred, Northern Brown, Southern Brown and Rufous Spiny Bandicoots. These two groups probably had broad overlap zones, although it is difficult to be certain of this now due to the widespread regional extinction of bandicoots that occurred in semi-arid areas after European settlement.

Among the humid zone species, the Long-nosed Bandicoot is centred on eastern and south-eastern Australia in closed and open forest and probably differentiated there. Absent from Tasmania, it probably had a more northerly centre of origin within the region and subsequently invaded the south-east after the separation of Tasmania. *Isoodon* has a predominantly northern Australian species, the Northern Brown Bandicoot, and a predominantly southern Australian one, the Southern Brown Bandicoot, both essentially open forest/grassland species ranging from the east to the west of the continent in their respective latitudes. The two species ranges meet, apparently with no overlap zone, at the Hawkesbury River in eastern New South Wales. Why each has failed to penetrate beyond the river is unclear. On Cape York Peninsula, the Rufous Spiny Bandicoot occurs as part of the faunal transition between New Guinea and Australia. The boundaries of these four species, other than at the Northern/Southern Brown Bandicoot contact zone at the Hawkesbury River, appear to be delimited by increasing aridity or factors associated with it, such as lack of suitable vegetation. A fifth species of the humid zone, The Eastern Barred Bandicoot, has a more limited distribution and occurs in a small area of the basalt grasslands and savannah woodlands of south-western Victoria (Seebeck 1979). It also occurs generally in Tasmania, where its habitat utilisation is much wider (Heinsohn 1966). The mainland distribution of the Eastern Barred Bandicoot seems to be delimited by interaction with Long-nosed Bandicoots (and Southern Brown Bandicoots). It is a species originating in semi-arid temperate grassland woodland that has been able to invade open forest and other areas of Tasmania secondarily in the absence of its presumed competitor, the Long-nosed Bandicoot.

The broad distributional patterns of the arid and semi-arid bandicoots are more difficult to interpret, due to taxonomic problems in Golden, Western Barred and Desert Bandicoot and poor documentation of their former distributions and biology. The Golden Bandicoot was primarily a species of northern and central latitudes, whereas the two *Perameles* species were centred on southern and

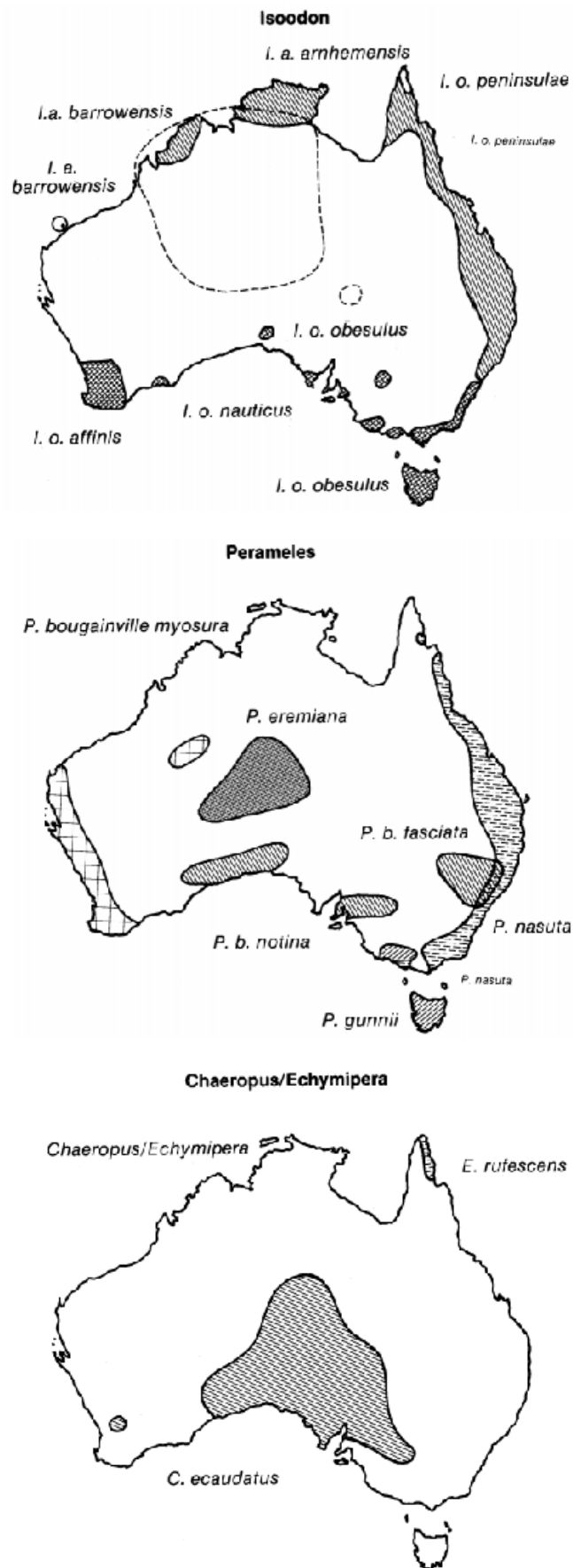


Figure 24.11 Distribution of Australian bandicoots. (Top) *Isoodon* spp.; (Middle) *Perameles* spp.; (Bottom) *Chaeropus* and *Echymipera*. Subspecies are shown for taxa where there is some taxonomic uncertainty.

central latitudes. As is the case with the Northern and Southern Brown Bandicoots, there is an implication here that northern and southern centres of origin were important to bandicoots or that latitudinal barriers were once important in separating populations. These arid species appear to have been ubiquitous, even penetrating well into the humid zone in some areas. Krefft (1866) refers to the Western Barred Bandicoot (as *P. fasciata*) occurring in the immediate neighbourhood of Sydney. Forms of the Golden Bandicoot occur in the Kimberley and Arnhem Land sympatric with Northern Brown Bandicoots and, possibly, even on Cape York Peninsula, if *Isoodon obesulus peninsulae* is interpreted as a member of the Golden Bandicoot group.

A dwarfed form of the Southern Brown Bandicoot, *I. o. nauticus*, has developed on Nuyts Archipelago off the South Australian coast. This may be a reflection of a poorer food supply or increased competition for food in an island population. There may also be slight dwarfing in the island form *I. auratus barrowensis* from Barrow Island, Western Australia. Marked size variation is present also in mainland Golden Bandicoots with the desert forms being smaller than those from the Kimberley and Arnhem Land. As with island forms, this may be an adaptation to poorer food resources.

The phenomenon of altitudinal species zonation exhibited by New Guinea species (Ziegler 1977), is absent among Australian bandicoots.

Peramelids contribute to the faunal transition between Australia and New Guinea. Of the New Guinea species, the Rufous Spiny Bandicoot extends onto Cape York Peninsula, occupying small rainforest patches and some adjacent vegetation types (Gordon & Lawrie 1977). Of the Australian bandicoots, only the Northern Brown Bandicoot intrudes into the grassland and grassy woodland of lowland southern New Guinea. These two incursions indicate that habitat is as important a factor in dividing the two groups of bandicoots as is the water barrier. Where suitable habitat exists, animals have managed to colonise the other landmass, despite its present geographic isolation. Failure of other species to occur on both landmasses indicates either that habitat is unsuitable for them or that barriers other than water were important. For high altitude New Guinean species, the lack of montane habitats on upper Cape York Peninsula would have presented a formidable barrier to movement into the rainforests of northeastern Australia.

Several problems exist in peramelid zoogeography, apart from those caused by the taxonomic confusion among some arid and semi-arid zone species. Australian species are ecologically flexible, whose broad patterns of distribution are determined particularly by climatic factors, such as rainfall gradients. Habitat utilisation is sufficiently broad in at least some species that habitat discontinuities do not form strong barriers to their distributions. A more detailed analysis of climatic data, such as seasonality and moisture index gradients (Nix 1982), may reveal the factors limiting their distributions. Similarly, there is a need for an understanding of the physiological constraints faced by humid species occurring at the limits of their distribution in semi-arid zones and of their ability to reproduce and gain sufficient nutrition in such areas. It is likely that these are the kind of factors that ultimately place limits on the spread of the humid zone species into the semi-arid zones.

An examination of sympatry among peramelids suggests that interspecific competition may place constraints on distribution. Most parts of Australia are, or were, occupied by one species or two sympatric species. If thylacomyids are included in the analysis and the largely herbivorous Pig-footed Bandicoot is excluded from consideration, humid zones mostly show a species diversity of two, semi-arid and arid zones mainly range from one to two (with a few areas

with three species; Morton & Baynes 1985) and Cape York Peninsula has three to four species (Gordon *et al.* 1990). The scanty information from New Guinea suggests that peramelid species diversities there tend to be high.

It is unusual in Australia for peramelid congeners to be sympatric, although this occurs for Northern Brown and Golden Bandicoots and *I. obesulus peninsulae* in some parts of northern Australia. So far as is known, Australian bandicoots show clear-cut habitat differences in areas of sympatry and habitat utilisation may change with species composition. The Eastern Barred Bandicoot (for example, see above) is able to use forest and shrubland in Tasmania (Heinsohn 1966), whilst being restricted to grassland and savannah in Victoria. Interspecific competition certainly must be considered if the zoogeography of perameloids is to be understood.

In the arid and semi-arid zones, the causes of the occurrence of Golden Bandicoots as a primarily northern and central species and Western Barred Bandicoots as a primarily southern species, is poorly understood. This may be a direct or indirect response to some aspect of climatic zonation of the continent, as discussed by Nix (1982). Finlayson (1961) associated the Golden Bandicoot with spinifex vegetation and its continental distribution correlates broadly with the spinifex zones; similarly, the Western Barred Bandicoot may be primarily a species of the shrub steppe vegetation of southern arid Australia. In the terminology of Nix (1982), these would be megatherm and mesotherm species, respectively.

The paucity of peramelid species in semi-arid and arid Queensland is difficult to interpret. Apart from the Bilby in southern and south-western Queensland, no semi-arid species were known from this area. Unless this is simply a collecting deficiency due to the rapid extinction of bandicoots after early settlement, it represents a puzzling anomaly in the otherwise successful adaptation of bandicoots to the Australian continent.

Affinities with other Groups

Perameloids exhibit a mix of primitive (such as polyprotodont dentition) and specialised (such as syndactyly) characters. This has generated the recurring concept that they form an evolutionarily intermediate group between primitive marsupials, such as dasyuroids and didelphoids, and the more advanced phalangeroids.

Much of the earlier controversy surrounded the use of higher taxonomic groupings. Bandicoots are polyprotodont, but syndactylous, whereas the South American caenolestids are diprotodont, but didactylous. If marsupials are fundamentally divided into either Polyprotodontia/Diprotodontia (see Thomas 1888) or Didactyla/Syndactyla (see Jones 1924), the peramelids or the caenolestids, respectively, have to have one or other apomorphy interpreted as convergence. Simpson (see Kirsch & Calaby 1977) solved some of the confusion by abandoning the higher taxa and classifying marsupials into superfamilies of equal standing, but this still left open the question of peramelid affinities.

Thomas (1888) revised the bandicoots and allied them closely to the Dasyuridae. He believed that bandicoot syndactyly had arisen independently from that of the diprotodonts because of the 'wholly polyprotodont character of the rest of their organisation, even down to the structure of their carpal and tarsal bones'. Contemporary workers largely support the concept of a close affinity of bandicoots with dasyurids. Bensley (1903), however, felt that bandicoots were more closely related to diprotodonts than dasyurids, and this view influenced many subsequent workers.

In recent years, peramelid affinities with South American groups have been given more attention. Archer (1976a, 1976b, 1976e) develops the proposal that peramelids were directly derived from didelphids and in turn, gave rise to diprotodonts. In this hypothesis, peramelids have no special relationship with dasyurids. This scenario is based on several lines of evidence. Peramelid teeth lack any particular similarities to those of dasyurids, but exhibit marked similarity to those of didelphids; in basicranial morphology, peramelids are most similar to didelphids and show no special affinity with dasyurids; and peramelid molars show similarities to those of selenodont diprotodontans which, in Archer's hypothesis, arose from peramelids and formed the base stock for all other diprotodont radiations.

Szalay (1982, cited in Archer 1984b) supports the South American affinities of peramelids, but derives them from the microbiotheriids, rather than the didelphids. On the basis of tarsal morphology, bandicoots and all the other major Australian lines were derived independently from a microbiotheriid ancestor.

At the time of Archer's work, serology was being developed as a taxonomic aid, leading to Kirsch's (1977a) finding that perameloids and dasyurids are closely related. Such work has had a significant influence on subsequent phylogenetic analysis; Archer (1984b) concluded that perameloids are a sister-group of the dasyurids on this basis. Baverstock *et al.* (1990), using an immunological technique (microcomplement fixation of albumin), found further support for this relationship and also conclude that peramelids and dasyurids together formed a sister-group to a number of diprotodont groups.

Unresolved issues include the more detailed resolution of peramelid/dasyurid relationships, the question of peramelid affinities with South American marsupials and the history of syndactyly. Hall (1981) questions whether syndactyly could have arisen independently in two lines of marsupials and suggests that it arose once only, in the Late Cretaceous or Paleocene, as a teratological reaction in marsupials switching from an insectivorous to a herbivorous diet. Tarsal morphology also suggests that syndactyly arose monophyletically as the peramelid foot structure may be easily derived from the simple dasyurid/phalangerid pattern (Marshall 1972).

A final controversy concerns the relationship of the peramelids to the thylacomyids (bilbies). The latter were initially treated as highly specialised peramelids (see Thomas 1888) and this practice was followed by Tate (1948). Bensley (1903), however, recognised their distinctiveness by placing them in the subfamily Thylacomyinae, particularly on the basis of their molar morphology (see above). Archer & Kirsch (1977), on the basis of serological, chromosomal and morphological evidence, elevated the taxon to familial rank. Baverstock *et al.* (1990), however, have found conflicting immunologic evidence that places bilbies close to other bandicoots and gives no support for a separate family. Groves & Flannery (1990), examining morphological data with cladistic techniques, also place bilbies close to other bandicoots.

Affinities within the Peramelidae

Living peramelids include a number of different adaptive types, although their ecological flexibility has ensured that they occupy a broader ecological niche than is suggested by a consideration of their morphology.

Isoodon species show adaptations for use of close ground cover and semi-arid to arid areas. They are stockily built with short ears, relatively short, broad hind feet, drab body coloration and auditory bullae that are both large and complex. It may be a megatherm genus (Nix 1982) that has succeeded in establishing in southern Australia. Most taxa occur in the northern parts of the generic range.

Perameles species show adaptations for the use of open habitat and arid through to humid areas. The ears are elongate, the feet relatively more elongate and the body is more lightly built than in *Isoodon*, transverse body bars are developed (apparently for disruptive camouflage) and auditory bullae range from large to small. The genus is primarily mesotherm (Nix 1982), apart from the extension of the Long-nosed Bandicoot into Queensland in closed forest and wet sclerophyll forest.

Echymipera species have spiny fur, an elongate rostrum (together with *Rhynchomeles* the muzzle is longest of all bandicoots), short, broad hind feet, a short naked tail and small ears. *Echymipera* and *Rhynchomeles* are rainforest genera specialised (for example, the elongate muzzle) for extracting food from small crevices.

The genera *Peroryctes* and *Microperoryctes* include the most plesiomorphic species (Archer 1984b). Some show elongation of the hind foot for running. They are generalised rainforest bandicoots. Because of its soft mole-like pelage, it has been suggested that *Microperoryctes murina* is a fossorial species (Tate & Archbold 1937).

Chaeropus ecaudatus has a herbivorous dentition and anatomy (see above), elongate limbs appropriate for running, elongate ears and large auditory bullae. It is a species of arid/semi-arid areas with herbivorous and cursorial specialisations.

Early workers on bandicoot taxonomy (such as Thomas 1888) perceived two main groups, the specialised genera *Macrotis* and *Chaeropus*, and the remainder, which were regarded as rather generalised. *Macrotis* was subsequently placed in another family (see above) and other generic concepts were gradually refined. Dental morphology, particularly with regard to the development of quadrate molars in groups such as *Isoodon*, *Macrotis* and *Chaeropus*, has received much attention in this process.

Tate (1948) based his phylogeny of the Peramelidae on their level of morphological specialisation. *Macrotis* and *Chaeropus* were placed distantly from each other and from the 'relatively unprogressive' remaining genera. *Isoodon* was then placed separately from the remainder because of its quadrate molars, large auditory bullae and shortened rostrum. *Echymipera* and *Rhynchomeles* were then considered to be separate from *Perameles*/*Peroryctes*/*Microperoryctes* because of the loss of the fifth incisor and a tendency to have an enlarged last premolar.

Baverstock *et al.* (1990) have preliminary immunological evidence that bandicoots generally fall into three groups - *Macrotis*, *Echymipera* and *Isoodon*/*Perameles*. Groves & Flannery (1990), using a cladistic analysis of mainly skull characters, propose two separate families to accommodate the New Guinea genera and the Australian genera. *Macrotis* is regarded as closely linked to *Chaeropus*. Both analyses agree on splitting up the generalized groups (*Perameles* and the New Guinea genera) and on the placement of *Macrotis*. The alliance of *Perameles* and *Isoodon* by Baverstock *et al.* is also of some significance.

Data from recent electrophoretic work on *Isoodon* have highlighted the complexity of the relationships between the different taxa of a group that is morphologically little differentiated (Close *et al.* 1990). The Northern Brown Bandicoot has distinct populations on the east coast and in northern Australia that appear not to interbreed in captivity. A third population, the New Guinea group, *I. m. moresbyensis*, has not yet been examined. In the Southern Brown Bandicoot group, *I. o. peninsulae* emerges as the most distinct taxon, while *I. obesulus* shows divisions between south-western and south-eastern

populations and affinities between *I. auratus barrowensis* and south-eastern *I. obesulus*. This situation suggests a recent history of population expansion, contraction, subsequent isolation and genetic differentiation of subpopulations.

Relationships and taxonomic status of populations of the Western Barred Bandicoot group have not been determined, but it is clear that problems exist there. The Desert Bandicoot appears to be an arid population with affinities to one of the other semi-arid/arid populations of the Western Barred Bandicoot group.

The major Australian climates are thought to have been present from the early Tertiary (Nix 1982) and we may postulate that the main adaptive groups of bandicoots arose early in their history. Baverstock suggests that the three groups, *Macrotis*, *Echymipera* and *Isoodon/Perameles*, separated in the Oligocene. If we extrapolate from the biology of modern species, then these represent semi-arid, rainforest and humid/semi-arid/arid lines, respectively. The most plesiomorphic and presumably the source stock of the bandicoot radiation, are species of either rainforest or of the most aseasonal habitats (Nix 1982). *Chaeropus* also may have arisen at this time as a semi-arid/arid group. Subsequently, as the continent dried during the Miocene, some faunal elements retreated to New Guinea and were preserved there (Archer 1984c).

Ziegler (1977) discussed factors affecting bandicoot radiation in New Guinea. In Australia, *Isoodon* and *Perameles* differentiated either in the Pliocene (Baverstock *et al.* 1990) or in the Late Miocene (here fossil *Perameles* and *Isoodon* are present; Rich 1982), perhaps as semi-arid groups or in response to the emerging sclerophyll vegetation. At some subsequent time, *Perameles* differentiated into rainforest and wet eucalypt forests (as *P. nasuta*) and *Echymipera* invaded rainforests on Cape York Peninsula.

Nix (1982) has argued that seasonality of rainfall and temperature, rather than aridity, have been major driving forces in evolutionary radiation in Australia. Peramelid radiation, so far as is known, is consistent with this view. There is evidence that latitudinal barriers have been important, corresponding to the division between megatherm and mesotherm climates.

Australian genera may be classified without too much difficulty as either mesotherm (*Chaeropus*, *Macrotis*, *Perameles*) or megatherm (*Isoodon*), the former category including the most specialised arid and semi-arid species. Tate (1948) considers the latter phenomenon to be evidence that greater environmental changes had taken place in the south of the continent than in the north during the Tertiary and perhaps the early arid environments were located in the mesotherm zone. From the foregoing and from a consideration of morphology, we may also argue that *Isoodon* arose as a megathermal group of semi-arid grasslands or other dense low cover and that *Perameles* arose as a mesothermal group of open habitats, perhaps semi-arid shrublands. *Isoodon* then differentiated into the *macrourus* and the *obesulus/auratus* groups in northern Australia, also later entering mesothermal areas, while *Perameles* differentiated primarily in mesothermal areas.

During the Quaternary, the climate is thought to have become drier and to have included some marked fluctuations between extremes of cool/dry and warm/wet periods. Faunal populations must have undergone marked expansions and contractions of their distribution. Several bandicoot groups show genetic differentiation with little morphological change (Northern Brown, Southern Brown and Golden Bandicoots and probably Western Barred Bandicoots) and this may be attributed to the fluctuating climates of the Tertiary.

Fossil Record

Peramelids are known in Australia as early as the Middle and Late Miocene, where the genera *Perameles*, *Peroryctes*, *Echymipera* and *Isoodon* have been recognised (Rich 1982). These and more recent fossils are of extant genera. Two undescribed genera, however, occur in the recently discovered Riversleigh fauna of the Middle Miocene (Archer 1984b). Archer, Clayton & Hand (1984) list Australian fossil bandicoots.

COLLECTION AND PRESERVATION

Collection

Bandicoots are commonly caught live in wireframe traps with either a treadle or hook-trigger mechanism baited with substances derived from vegetable oils and meat fats. Common baits are bread and peanut butter, rolled oats and peanut butter, leather soaked in linseed oil and bread and dripping.

Trappability varies with age and with experience in Northern Brown Bandicoots. Young become trappable at a mean age of 165 days (range 104 to 255). Adults habituate to being trapped after their first capture. First capture, however, is difficult in some animals. Some animals, on exposure to trapping, show a slight short-term increase in trappability and others show the reverse (Gordon 1971).

There are also indications that trappability varies between species and regions. Long-nosed Bandicoots may be more difficult to trap than Northern Brown Bandicoots. The latter appears more difficult to capture in tropical Queensland than in southern Queensland. Availability of alternative wild foods in different areas may influence trappability in these instances.

Laboratory Care

Bandicoots are easily kept in captivity and breed readily, given the right conditions (Lyne 1971; MacKerras & Smith 1960; Merritt 1970; Seebeck 1979; Stodart 1966a).

Space is important in minimising conflict between animals and in permitting breeding. Cages of 25m² or larger are advisable. Foods such as the various solid pellets for laboratory animals and dry dog food are suitable staples for keeping caged animals, though supplements are advisable, preferably including insects. Northern Brown Bandicoots kept solely on rat pellets may show a lightening of the coat colour, indicating some nutritional deficiency.

CLASSIFICATION

Peroryctes broadbenti (Ramsay, 1878) New Guinea

Peroryctes longicauda (Peters & Doria, 1876) New Guinea

Peroryctes papuensis Laurie, 1952 New Guinea

Peroryctes raffrayanus (Milne-Edwards, 1878) New Guinea

Microperoryctes murina Stein, 1932 New Guinea

Perameles bougainville Quoy & Gaimard, 1824

Perameles eremiana Spencer, 1897

Perameles gunnii Gray, 1838

Perameles nasuta Geoffroy, 1804

Echymipera clara Stein, 1932 New Guinea

Echymipera kalubu (Lesson, 1828) New Guinea

Echymipera rufescens (Peters & Doria, 1875) New Guinea and Australia

Rhynchomeles prattorum Thomas, 1920 New Guinea

Isoodon auratus (Ramsay, 1887)

Isoodon macrourus (Gould, 1842)

Isoodon obesulus (Shaw, 1797)

Chaeropus ecaudatus (Ogilby, 1838)

Descriptions of Genera

Peroryctes: Incisors 5/3, upper molars trituberculate; bullae small, hemispherical, more or less incomplete, less than 5 mm wide x 10 mm long; condylobasal length usually greater than 44 mm; large hind feet usually greater than 38 mm long, soles of feet granular; small ears, antihelix process relatively short; pelage slightly hispid, some species with body stripes; relatively long tail, usually greater than 120 mm (Ziegler & Lidicker 1968).

Microperoryctes: Incisors 5/3, upper molars trituberculate; bullae small, hemispherical, more or less incomplete, less than 5 mm wide x 10 mm long; condylobasal length usually less than 44 mm, highly fenestrated palate; hind feet less than 38 mm, soles of feet granular; small ears, antihelix process relatively short; pelage soft, dense, not spinous, some populations with dorsal stripe; short tail, usually less than 120 mm (Ziegler & Lidicker 1968).

Perameles: Incisors 5/3, upper molar simple, trituberculate; bullae small to moderate in size, hemispherical, complete; mean condylobasal length 77 mm (female) to 85 mm (male); ears elongate, 35—54 mm; pelage slightly hispid, barred rump in most species; tail relatively short, 60—180 mm, brown dorsal tail stripe in some species (Freedman & Joffe 1967a).

Echymipera: Incisors 4/3, upper molars trituberculate to quadrituberculate, inner lobe of M^4 extends farther medially than inner lobe of M^3 ; bullae small, hemispherical, more or less incomplete, less than 5 mm wide x 10 mm long; rostrum elongated; hind feet relatively broad with hyperdevelopment of tarsal pad behind digits IV/V in some species, soles granular; small ears, antihelix process relatively short; pelage quite spinous, colour noticeably lighter below than above; tail short, less than 125 mm (Ziegler & Lidicker 1968).

Rhynchomeles: Incisors 4/3, upper molars trituberculate, hypocone nearly obsolete, inner lobe of M^4 reduced, not extending as far medially as inner lobe of M^3 , teeth generally small, delicate, widely spaced, PM^3 robust; bullae small, hemispherical, more or less incomplete, less than 5 mm wide x 10 mm long; great elongation of rostrum, skull long and slender; hind feet about 65 mm, soles granular; ears short, oval, antihelix process relatively short; pelage soft, non-spinous, dark chocolate brown above and only slightly paler below with white spot on chest; tail greater than 125 mm; restricted to Ceram Island (Ziegler & Lidicker 1968).

Isoodon: Incisors 5/3, upper molars quadrituberculate; bullae large, complete, pear-shaped, greater than 5 mm wide x 10 mm long; rostrum relatively short; hind feet relatively broad, soles of feet not granular but smooth, cobblestone-like or transversely wrinkled; ears short, oval, antihelix process long, rounded and often appearing twisted; pelage hispid; tail relatively short (Ziegler & Lidicker 1968).

Chaeropus: Incisors 5/3, stout and relatively broad rather than flattened and blade-like, upper molars quadrituberculate, I⁵ close or adjacent to other incisors, upper canine is premolariform, last upper premolar smaller than preceding one; bullae small, hemispherical, more or less complete; skull relatively short and broad, slightly more than half as wide as long; hind feet elongate, specialised for cursorial life as described above; ears elongate, 52—60 mm; pelage hispid; tail relatively long, 100—139 mm, with small crest.

LITERATURE CITED

- Archer, M. (1975). Abnormal dental development and its significance in dasyurids and other marsupials. *Memoirs of the Queensland Museum* 17: 251–265
- Archer, M. (1976a). The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhyaenids, (Marsupicarnivora) and peramelids (Peramelina; Marsupialia). *Australian Journal Zoology, Supplementary Series* 39: 1–34
- Archer, M. (1976b). The basicranial region of marsupicarnivores (Marsupialia), interrelationships of carnivorous marsupials, and affinities of the insectivorous marsupial peramelids. *Zoological Journal of the Linnean Society* 59: 217–322
- Archer, M. (1976e). Phascolarctid origins and the potential of the selenodont molar in the evolution of diprotodont marsupials. *Memoirs of the Queensland Museum* 17: 367–371
- Archer, M. (1981a). Results of the Archbold Expeditions. No. 104. Systematic revision of the marsupial dasyurid genus *Sminthopsis* Thomas. *Bulletin of the American Museum of Natural History* 168: 61–224
- Archer, M. (1984b). The Australian marsupial radiation. Pp. 633–808 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Archer, M. (1984c). Evolution of arid Australia and its consequences for vertebrates. Pp. 97–108 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Archer, M. & Kirsch, J.A.W. (1977). The case for the Thylacomyidae and Myrmecobiidae, Gill, 1872, or why are marsupial families so extended? *Proceedings of the Linnean Society of New South Wales* 102: 18–25
- Archer, M., Clayton, G. & Hand, S. (1984). A checklist of Australasian fossil mammals. Pp. 1027–1082 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Barnes, A. & Gemmell, R.T. (1984). Correlations between breeding activity in the marsupial bandicoots and some environmental variables. *Australian Journal of Zoology* 32: 219–226
- Baverstock, P.R., Flannery, T., Aplin, K., Birrell, J. & Kreig, M. (1990). Albumin immunologic relationships of the bandicoots (Perameloidea: Marsupialia) - a preliminary report. Pp. 13–18 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW
- Bensley B.A. (1903). On the evolution of the Australian Marsupialia; with remarks on the relationships of the marsupials in general. *Transactions of the Linnean Society of London, second series, Zoology* 9: 83–217

- Braithwaite, R.W. (1977). Preliminary observations on the movement patterns of *Rattus lutreolus* and other Victorian small mammals. *Victorian Naturalist* 94: 216–219
- Braithwaite, R.W. & Gullan, P.K. (1978). Habitat selection by small mammals in a Victorian heathland. *Australian Journal of Ecology* 3: 109–127
- Brunner, H. & Coman, B.J. (1974). *The Identification of Mammalian Hair*. Inkata Press : Melbourne ix 176 pp.
- Buchman, O.L.K. & Grecian, E.A. (1974). Discrimination-reversal learning in the marsupial *Isoodon obesulus* (Marsupialia, Peramelidae). *Animal Behaviour* 22: 975–981
- Burger, C.H. & Cross, R.B. (1982). Aspects of renal vascular organization and early vascular tubular relations of the marsupial *Isoodon obesulus*. *Anatomical Record* 203: 47–54
- Calaby, J.H. (1966). Mammals of the upper Richmond and Clarence Rivers, New South Wales. *CSIRO Division of Wildlife Research Technical Paper* No. 10 55 pp.
- Close, R.L. (1977). Recurrence of breeding after cessation of suckling in the marsupial *Perameles nasuta*. *Australian Journal of Zoology* 25: 641–645
- Close, R.L. (1984). Rates of sex chromosome loss during development in different tissues of the bandicoots *Perameles nasuta* and *Isoodon macrourus* (Marsupialia: Peramelidae). *Australian Journal of Biological Science* 37: 53–61
- Close, R.L., Murray, J.D. & Briscoe, D.A. (1990). Electrophoretic and chromosome surveys of the taxa of short-nosed bandicoots within the genus *Isoodon*. Pp. 19–27 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW
- Dahl, K. (1897). Biological notes on North-Australian mammalia. *The Zoologist* (4)1: 189–216
- Day, B., Kirkby, R. & Stenhouse, H. (1974). The behaviour of marsupials III. The short-nosed bandicoot, *Isoodon macrourus* (Peramelidae), in the open field. *Australian Mammalogy* 1: 255–259
- Dixon, J.M. (1978). Taxonomy of short-nosed bandicoots of the genus *Isoodon* (Marsupialia: Peramelidae), based on cranial characteristics. p. 79 Abstract of papers, International Congress of Theriology 2 Brno 1978
- Dixon, J.M. (1981). Selection of a neotype for the southern short-nosed (brown) bandicoot, *Isoodon obesulus* (Shaw & Nodder, 1797). *Victorian Naturalist* 98: 130–135
- Dixon, J.M. & Huxley, L. (1985). *Donald Thomson's Mammals and Fishes of Northern Australia*. Nelson Publishers : Melbourne 210 pp.
- Dunnet, G.M. & Mardon, D.K. (1974). A monograph of Australian fleas (Siphonaptera). *Australian Journal of Zoology Supplementary Series* 30: 1–273
- Finlayson, H.H. (1935a). On mammals from the Lake Eyre Basin: Part II The Peramelidae. *Transactions of the Royal Society of South Australia* 59: 227–236
- Finlayson, H.H. (1961). On central Australian mammals. Part IV - The distribution and status of central Australian species. *Records of the South Australian Museum* 14: 141–191
- Fosse, G. & Risnes, S. (1972a). Development of the teeth in a pouch-young specimen of *Isoodon obesulus* and one of *Perameles gunnii* (Peramelidae: Marsupialia). *Archives in Oral Biology* 17: 829–838
- Fosse, G. & Risnes, S. (1972b). Development of the incisors in two pouch-young stages of *Isoodon macrourus*. *Archives in Oral Biology* 17: 839–845

- Freedman, L. (1967). Skull and tooth variation in the genus *Perameles* Part 1: Anatomical features. *Records of the Australian Museum* 27: 147–166
- Freedman, L. & Joffe, A.D. (1967a). Skull and tooth variation in the genus *Perameles* Part 2: Metrical features of *P. nasuta*. *Records of the Australian Museum* 27: 183–195
- Freedman, L. & Joffe, A.D. (1967b). Skull and tooth variation in the genus *Perameles* Part 3: Metrical features of *P. gunnii* and *P. bougainville*. *Records of the Australian Museum* 27: 197–212
- Freeman, L. & Rightmire, G.P. (1971). Skull and tooth variation in Australian bandicoots (Peramelidae, Marsupialia): the genus *Isodon* and multivariate comparisons with *Perameles*. *Journal of the Royal Society of Western Australia* 54: 21–31
- Friend, G.R. (1990). Breeding and population dynamics of *Isodon macrourus* (Marsupialia: Peramelidae): Studies from the wet-dry tropics of northern Australia. Pp. 357–365 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW
- Friend, G.R. & Taylor, J.A. (1985). Habitat preferences of small mammals in tropical open-forest of the Northern Territory. *Australian Journal of Ecology* 10: 173–185
- Frith, H.J. (1973). *Wildlife Conservation*. Angus & Robertson : Sydney xiv 414 pp.
- Gemmell, R.T. (1979). The fine structure of the luteal cells in relation to the concentration of progesterone in the plasma of the lactating bandicoot *Isodon macrourus* (Marsupialia: Peramelidae). *Australian Journal of Zoology* 27: 501–510
- Gemmell, R.T. (1981). The role of the corpus luteum of lactation in the bandicoot *Isodon macrourus* (Marsupialia: Peramelidae). *General and Comparative Endocrinology* 44: 13–19 [17]
- Gemmell, R.T. (1982). Breeding bandicoots in Brisbane (*Isodon macrourus*; Marsupialia, Peramelidae). *Australian Mammalogy* 5: 187–193
- Gemmell, R.T. & Johnston, G. (1985). The development of thermoregulation and the emergence from the pouch of the marsupial bandicoot *Isodon macrourus*. *Physiological Zoology* 58: 299–302
- Gemmell, R.T., Jenkin, G. & Thorburn, G.D. (1980). Plasma concentrations of progesterone and 13, 14-dihydro-15 keto-prostaglandin F₂ at parturition in the bandicoot, *Isodon macrourus*. *Journal of Reproduction and Fertility* 60: 253–256
- Gordon, G. (1971). A study of island populations of the short-nosed bandicoot *Isodon macrourus* Gould. Unpubl. PhD Thesis, Sydney, University of New South Wales viii 170 pp.
- Gordon, G. (1974). Movements and activity of the short-nosed bandicoot *Isodon macrourus* Gould (Marsupialia). *Mammalia* 38: 405–431
- Gordon, G. (1984). Bandicoots and bilbies. Pp. 846–849 in Macdonald, D. (ed.) *The Encyclopedia of Mammals*. Allen & Unwin : London Vol. 2
- Gordon, G. & Lawrie, B.C. (1977). The rufescent bandicoot, *Echymipera rufescens* (Peters & Doria) on Cape York Peninsula. *Australian Wildlife Research* 5: 41–45
- Gordon, G., Hall, L.S. & Atherton, R.G. (1990). The status of bandicoots in Queensland. Pp. 37–42 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW

- Green, L.M.A. (1963a). Distribution and comparative histology of cutaneous glands in certain marsupials. *Australian Journal of Zoology* 11: 250–272
- Griffiths, M.E. (1968). *Echidnas*. Pergamon Press : Oxford ix 282 pp.
- Groves, C. & Flannery, T. (1990). A review of the families and genera of bandicoots. P?????????????p. 1-11 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW
- Hall, L.S. (1981). The problem with syndactyly in marsupials. *Bulletin of the Australian Mammal Society* 7: 36–37
- Hall, L.S. (1983b). Observations of body weight and breeding of the northern brown bandicoot, *Isoodon macrourus*, trapped in south-east Queensland. *Australian Wildlife Research* 10: 467–476
- Hall, L.S. (1990). Growth and a description of the development of external features of pouch young of captive *Isoodon macrourus*. P ?????????????????? p. 123-133 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW
- Hall, L.S. & Hughes, R.L. (1985). The embryological development and cytodifferentiation of the anterior pituitary in the marsupial *Isoodon macrourus*. *Anatomy & Embryology* 172: 353–363
- Harrison, J.L. (1962a). The food of some Innisfail mammals. *Proceedings of the Royal Society of Queensland* 73: 37–43
- Harrison, J.L. (1962b). Mammals of Innisfail I: species and distribution. *Australian Journal of Zoology* 10: 45–83
- Hayman, D.L. & Martin, P.G. (1974). *Mammalia I: Monotremata and Marsupialia*. In John, B. (ed.) *Animal Cytogenetics, Vol. 4, Chordata* 4. iv + 110 pp. Gebruder Borntraeger : Berlin
- Hearn, J.P. (1974). The pituitary gland and implantation in the female tammar wallaby *Macropus eugenii*. *Journal of Reproduction and Fertility* 39: 235–241
- Heinsohn, G.E. (1966). Ecology and reproduction of the Tasmanian bandicoots (*Perameles gunnii* and *Isoodon obesulus*). *University of California Publications in Zoology* 80: 1–107
- Hill, J.P. (1897). The placentation of *Perameles*. (Contributions to the embryology of marsupials - I). *Queensland Journal of Microscopical Science* 40: 385–446
- Hill, J.P. (1899). Contributions to the morphology and development of the female urogenital organs in the Marsupialia. I. On the female urogenital organs of *Perameles*, with an account of the phenomenon of parturition. *Proceedings of the Linnean Society of New South Wales* 24: 42–82
- Hill, W.C.O. & Rewell, R.E. (1954). The caecum of monotremes and marsupials. *Transactions of the Zoological Society of London* 28: 185–240
- Hollis, D.E. & Lyne, A.G. (1980). Ultrastructure of luteal cells in fully formed and regressing corpora lutea during pregnancy and lactation in the marsupials *Isoodon macrourus* and *Perameles nasuta*. *Australian Journal of Zoology* 28: 195–211
- Hughes, R. L., Hall, L. S., Archer, M. and Aplin, K. (1990). Observations on placentation and development in *Echymipera kalubu*. Pp. 259–270 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW.
- Hughes, R.L. (1962b). Role of the corpus luteum in marsupial reproduction. *Nature* 194: 890–891

- Hughes, R.L. (1965). Comparative morphology of spermatozoa from five marsupial families. *Australian Journal of Zoology* 13: 533–543
- Hughes, R.L. (1984). Structural adaptations of the eggs and the fetal membranes of monotremes and marsupials for respiration and metabolic exchange. Pp. 389–421 in Seymour, R.S. (ed.) *Respiration and Metabolism of Embryonic Vertebrates*. Junk : Dordrecht
- Hulbert, A.J. & Augée, M.L. (1982a). A comparative study of thyroid function in monotreme, marsupial, and eutherian mammals. *Physiological Zoology* 55: 220–228
- Hulbert, A.J. & Dawson, T.J. (1974a). Standard metabolism and body temperature of perameloid marsupials from different environments. *Comparative Biochemistry and Physiology* 47A: 583–590
- Hulbert, A.J. & Dawson, T.J. (1974b). Thermoregulation in perameloid marsupials from different environments. *Comparative Biochemistry and Physiology* 47A: 591–616
- Hulbert, A.J. & Dawson, T.J. (1974c). Water metabolism in perameloid marsupials from different environments. *Comparative Biochemistry and Physiology* 47A: 617–633
- Hulbert, A.J. & Gordon, G. (1972). Water metabolism of the bandicoot *Isodon macrourus* (Gould) in the wild. *Comparative Biochemistry and Physiology* 41A: 27–34
- Hume, I.D. (1982). *Digestive Physiology and Nutrition of Marsupials*. Cambridge University Press : Cambridge 256 pp.
- Jaeger, E.C. (1955). *A Source-book of Biological Names and Terms*. C.C. Thomas : Springfield xxxv 323 pp.
- Johnston, G.M. & Gemmell, R.T. (1987). Thyroid development in the marsupial bandicoot *Isodon macrourus*. *Anatomical Record* 217: 178–187
- Jones, F. Wood (1923a). *The Mammals of South Australia*. Part I. The Monotremes and the Carnivorous Marsupials (The Ornithodelphia and didactylous Didelphia). Government Printer : Adelaide pp. 1-131
- Jones, F. Wood (1924). *The Mammals of South Australia*. Part II Government Printer : Adelaide pp. 133-270
- Jones, F. Wood (1925). *The Mammals of South Australia*. Part III Government Printer : Adelaide pp. 271-458
- Kerry, K.R. (1969). Intestinal disaccharidase activity in a monotreme and eight species of marsupials (with an added note on the disaccharidases of five species of sea birds). *Comparative Biochemistry and Physiology* 29: 1015–1022
- Kingsmill, E. (1962). An investigation of criteria for estimating age in the marsupials *Trichosurus vulpecula* Kerr and *Perameles nasuta* Geoffroy. *Australian Journal of Zoology* 10: 597–616
- Kirsch, J.A.W. (1977a). A comparative serology of the Marsupialia, and a classification of the marsupials. *Australian Journal of Zoology Supplementary Series* 52: 1-152
- Kirsch, J.A.W. & Calaby, J.H. (1977). The species of living marsupials: an annotated list. Pp. 9–26 in Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. Macmillan : London
- Krefft, G. (1862). On the vertebrated animals of the lower Murray and Darling, their habits, economy, and geographical distribution. *Transactions of the Philosophical Society of New South Wales* 1862-1865: 1-38
- Lee, A.K. & Cockburn, A. (1985). *Evolutionary Ecology of Marsupials*. Cambridge University Press : Cambridge viii 274 pp.

- Lidicker, W.Z. & Follet, W.I. (1968). *Isoodon Desmarest* 1817, rather than *Thylacis Illiger* 1811, as the valid generic name of the short-nosed bandicoots (Marsupialia: Peramelidae). *Proceedings of the Biological Society of Washington* 81: 251–256
- Lyne, A.G. (1951). Notes on external characters of the barred bandicoot (*Perameles gunnii* Gray) with special reference to the pouch young. *Proceedings of the Zoological Society of London* 121: 587–598
- Lyne, A.G. (1952). Notes on the external characters of the pouch young of four species of bandicoot. *Proceedings of the Zoological Society of London* 122: 625–649
- Lyne, A.G. (1957). The development and replacement of pelage hairs in the bandicoot *Perameles nasuta* Geoffroy (Marsupialia: Peramelidae). *Australian Journal of Biological Sciences* 10: 197–216
- Lyne, A.G. (1964). Observations on the breeding and growth of the marsupial *Perameles nasuta* Geoffroy, with notes on other bandicoots. *Australian Journal of Zoology* 12: 322–339
- Lyne, A.G. (1971). Bandicoots in captivity. *International Zoo Yearbook* 11: 41–43
- Lyne, A.G. (1974b). Gestation period and birth in the marsupial *Isoodon macrourus*. *Australian Journal of Zoology* 22: 303–309
- Lyne, A.G. (1976). Observations on oestrus and the oestrous cycle in the marsupials *Isoodon macrourus* and *Perameles nasuta*. *Australian Journal of Zoology* 24: 513–521
- Lyne, A.G. (1981). Activity rhythms in the marsupials *Isoodon macrourus* and *Perameles nasuta* in captivity. *Australian Journal of Zoology* 29: 821–838
- Lyne, A.G. & Hollis, D.E. (1976). Early embryology of the marsupials *Isoodon macrourus* and *Perameles nasuta*. *Australian Journal of Zoology* 24: 361–382
- Lyne, A.G. & Hollis, D.E. (1979). Observations on the corpus luteum during pregnancy and lactation in the marsupials *Isoodon macrourus* and *Perameles nasuta*. *Australian Journal of Zoology* 27: 881–899
- Lyne, A.G. & Hollis, D.E. (1982). Observations on the lateral vaginae and birth canals in the marsupials *Isoodon macrourus* and *Perameles nasuta* (Mammalia). *Journal of Zoology, London* 198: 263–277
- Lyne, A.G. & Mort, P.A. (1981). A comparison of skull morphology in the marsupial bandicoot genus *Isoodon*: its taxonomic implication and notes on a new species, *Isoodon arnhemensis*. *Australian Mammalogy* 4: 107–133
- MacDonald, B. & Hughes, R.L. (1977). Plasma testosterone levels and ultrastructural studies of the prostate gland following castration in the marsupial *Isoodon macrourus*. *Theriogenology* 8: 195
- Mackerras, I.M. & Mackerras, M.J. (1960). Taxonomy of the common short-nosed marsupial bandicoot of eastern Queensland. *Australian Journal of Science* 23: 51–52
- Mackerras, I.M., Mackerras, M.J. & Sandars, D.F. (1953). Parasites of the bandicoot, *Isoodon obesulus*. *Proceedings of the Royal Society of Queensland* 63: 61–63
- Mackerras, J.J. (1959). Catalogue of Australian mammals and their recorded internal parasites. I-IV. Part I. Monotremes and Marsupials (pp. 101-125). Part II. Eutheria (pp. 126-143). Part III. Introduced Herbivora and the Domestic Pig (pp. 143-153). Part IV. Man (pp. 153-160). *Proceedings of the Linnean Society of New South Wales* 83: 101-160
- Mackerras, M.J. & Smith, R.H. (1960). Breeding the short-nosed marsupial bandicoot, *Isoodon macrourus* (Gould) in captivity. *Australian Journal of Zoology* 8: 371–382

- Marshall, L.G. (1972). Evolution of the peramelid tarsus. *Proceedings of the Royal Society of Victoria* 85: 51–60
- Martin, P.G. & Hayman, D.L. (1967). Quantitative comparisons between the karyotypes of Australian marsupials from three different superfamilies. *Chromosoma (Berlin)* 20: 290–310 [19]
- McFarlane, J. R., Carrick, F. N., Gemmell, R. T. and MacDonald, B. (1990). Seasonal effects on androgen secretion the male northern brown bandicoot, *Isoodon macrourus*. Pp. 251–257 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW.
- McKeown, K.C. (1951). Note on the food of a bandicoot. *Proceedings of the Royal Zoological Society of New South Wales* 1949–50: 42–43
- Menzies, J.I. (1972). The relative abundance of *Planigale novaeguineae* and other small mammals in the South Papuan savannas. *Mammalia* 36: 400–405
- Merchant, J. C. (1990). Aspects of lactation in the northern brown bandicoot *Isoodon macrourus*. Pp. 219–228 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW.
- Merritt, D.A. (1970). Observations on the short-nosed bandicoot at Lincoln Park Zoo, Chicago. *International Zoo Yearbook* 10: 130–131
- Miller, W.A. (1977). Extreme tooth loss in a specimen of *Isoodon macrourus* (Peramelidae: Marsupialia). *Australian Wildlife Research* 4: 229–232
- Morton, S.R. & Baynes, A. (1985). Small mammal assemblages in arid Australia: a reappraisal. *Australian Mammalogy* 8: 159–169
- Nix, H. (1982). Environmental determinants of biogeography and evolution in Terra Australis. Pp. 47–66 in Barker, W.R. & Greenslade, P.J.M. (eds) *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications : Frewville
- Padykula, H.A. & Taylor, J.M. (1976). Ultrastructural evidence for loss of the trophoblastic layer in the chorioallantoic placenta of Australian bandicoots (Marsupialia: Peramelidae). *Anatomical Record* 186: 357–386
- Padykula, H.A. & Taylor, J.M. (1977). Uniqueness of the bandicoot chorioallantoic placenta (Marsupialia: Peramelidae). Cytological and evolutionary interpretations. Pp. 303–323 in Calaby, J.H. & Tyndale-Biscoe, C.H. (eds) *Reproduction and Evolution*. Australian Academy of Science : Canberra
- Parsons, F.G. (1903). On the anatomy of the pig-footed bandicoot. *Journal of the Linnaean Society (Zoology)* 29: 64–80
- Rich, T.H. (1983). Monotremes, placentals and marsupials: their record in Australia and its biases. Pp. 385–477 in Rich, P.V. & Thompson, E.M. (eds) *The Fossil Vertebrate Record of Australasia*. Monash University Offset Printing Unit : Clayton
- Roberts, F.H.S. (1970). *Australian Ticks*. CSIRO : Melbourne iii 267 pp.
- Robertshaw, J.D. & Harden, R.H. (1985). The ecology of the dingo in north-eastern New South Wales. II. Diet. *Australian Wildlife Research* 12: 39–50
- Russell, E.M. & Pearce, G.A. (1971). Exploration of novel objects by marsupials. *Behaviour* 40: 312–322
- Sanders, D.F. (1952). Bandicoot food. *Proceedings of the Royal Society of Queensland* 62: 33
- Sapsford, C.S., Rae, C.A. & Cleland, K.W. (1969a). Ultrastructural studies on maturing spermatids and on Sertoli cells in the bandicoot *Perameles nasuta* Geoffroy (Marsupialia). *Australian Journal of Zoology* 17: 195–292

- Seebeck, J.H. (1979). Status of the barred bandicoot, *Perameles gunnii* in Victoria: with a note on husbandry of a captive colony. *Australian Wildlife Research* 6: 255–264
- Sharman, G.B. (1965). Marsupials and the evolution of viviparity. Pp. 1-28 in Carthy, J.D. & Duddington, C.L. (eds) *Viewpoints in Biology*. Butterworths : London
- Spencer, B. (1897). Description of two new species of marsupials from central Australia. *Proceedings of the Royal Society of Victoria* 9: 5–11
- Stodart, E. (1966a). Management and behaviour of breeding groups of the marsupial *Perameles nasuta* Geoffroy in captivity. *Australian Journal of Zoology* 14: 611–623
- Stodart, E. (1977). Breeding and behaviour of Australian bandicoots. Pp. 179–191 in Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. Macmillan : London
- Stoddart, D.M. (1980). Observations on the structure and function of cephalic skin glands in bandicoots (Marsupialia: Peramelidae). *Australian Journal of Zoology* 28: 33–41
- Stoddart, D.M. & Braithwaite, R.W. (1979). A strategy for utilization of regenerating heathland habitat by the brown bandicoot (*Isodon obesulus*; Marsupialia, Peramelidae). *Journal of Animal Ecology* 48: 165–179
- Strahan, R. (ed). (1983). *The Australian Museum Complete Book of Australian Mammals*. The National Photographic Index of Australian Wildlife. Angus & Robertson : Sydney xx 530 pp.
- Szalay, F.S. (1982a). A new appraisal of marsupial phylogeny and classification. Pp. 621–640 in Archer, M. (ed.) *Carnivorous Marsupials*. Royal Zoological Society of New South Wales : Sydney Vol. 2
- Tate, G.H.H. (1948). Results of the Archbold Expeditions. No. 60. Studies in the Peramelidae (Marsupialia). *Bulletin of the American Museum of Natural History* 92: 313–346
- Tate, G.H.H. (1952b). Results of the Archbold Expeditions. No. 66 Mammals of Cape York Peninsula, with notes on the occurrence of rain forest in Queensland. *Bulletin of the American Museum of Natural History* 98: 567–616
- Tate, G.H.H. & Archbold, R. (1937). Results of the Archbold Expeditions. No. 16. Some marsupials of New Guinea and Celebes. *Bulletin of the American Museum of Natural History* 73: 331–476
- Tedman, R. A. (1990). Some observations on the visceral anatomy of the bandicoot *Isodon macrourus* (Marsupialia: Peramelidae). Pp. 107–116 in Seebeck, J.H., Brown, P.R., Wallis, R.L. and Kemper, C.M. (eds) *Bandicoots and Bilbies*. Surrey Beatty : Chipping Norton, NSW.
- Thomas, O. (1888). Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum of Natural History. British Museum : London xii 401 pp.
- Thomas, O. (1906a). On mammals collected in south-western Australia for Mr W.E. Balston. *Proceedings of the Zoological Society of London* 1906: 468–478
- Triggs, B., Brunner, H. & Cullen, J.M. (1984). The food of fox, dog, and cat in Croajingalong National Park, south-eastern Victoria. *Australian Wildlife Research* 11: 491–499
- Troughton, E. le G. (1954). *Furred Animals of Australia*. Angus & Robertson : Sydney 5th edn xxxii 376 pp.

- Ullmann, S.L. (1979). Observations on the primordial oocyte of the bandicoot *Isoodon macrourus* (Peramelidae, Marsupialia). *Journal of Anatomy* 128: 619–631
- Van der Feen, P.J. (1962). Catalogue of the Marsupialia from New Guinea, the Moluccas and Celebes in the Museo Civico Di Storia Naturale Giacomo Doria in Genoa. *Annali Museo Civico di Storia Naturale Genova* 73: 19–70
- Walker, E.P. (1975). *Mammals of the World*. Vol. 1. Johns Hopkins University Press : Baltimore 3rd edn xlviii 646 pp.
- Watts, C.H.S. (1974c). The Nuyt's Islands bandicoot (*Isoodon obesulus nauticus*). *South Australian Naturalist* 49: 20–24
- Whittell, H.M. (1954). John Gilbert's notebook on marsupials. *Western Australian Naturalist* 4: 104–114
- Ziegler, A.C. & Lidicker, W.Z. Jnr (1968). Keys to the genera of New Guinea recent land mammals. *Proceedings of the California Academy of Science* 4th series: 33–71
- Ziegler, A.C. (1977). Evolution of New Guinea's marsupial fauna in response to a forested environment. Pp. 117–138 in Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. University Park Press : Baltimore [28]