



FAUNA *of* AUSTRALIA

30. POTOROIDAE

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Burrowing Bettong—*Bettongia lesueur* [CSIRO Wildlife & Ecology]



Desert Rat-Kangaroo—*Caloprymnus campestris* [F. Knight/ANPWS]

DEFINITION AND GENERAL DESCRIPTION

The Potoroidae is represented by two modern subfamilies, the Hypsiprymnodontinae, containing one extant and one described fossil form and the Potoroinae, containing nine [now eight (ed.)] extant and three described fossil forms. Together they contain the rat-kangaroos, bettongs and potoroos. The Palaeopotoroinae, the Propleopinae and the Bulungamyinae are known only from fossils and contain eight described taxa.

The Hypsiprymnodontinae is distinguished externally from the Potoroinae by the presence of a first pedal digit, a naked, scaly tail and a non-saltatory gait. The Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, has a simple stomach; members of the Potoroinae studied thus far have complex stomachs (I.D. Hume personal communication).

All modern potoroids are small, compact animals, with variously elongate muzzles, short rounded ears and short, but muscular forearms bearing small paws with short, forward-pointing spatulate claws. The hind limbs are well developed and heavily muscled with relatively elongate tibiae and fibulae, although in *Hypsiprymnodon* species the relative disparity in proportions between hind limbs and forelimbs is not as great. The hind feet are elongate. In *Hypsiprymnodon* the first toe has been retained, so there are five pedal digits, but in all Potoroinae there are only four. Digits II and III are weakly developed and joined in syndactyly; the major toe is digit IV. In *Hypsiprymnodon*, the tail is scaly; in all Potoroinae it is fully furred and a terminal crest is developed in some *Bettongia* species. It is weakly prehensile in some species of *Bettongia* and partially so in *Potorous* species.



Figure 30.1 *Bettongia* collecting nest material to be carried using its prehensile tail. (© ABRS) [K. Hollis]

HISTORY OF DISCOVERY

All modern genera had been recognised by 1876, when the Musky Rat-kangaroo, *Hypsiprymnodon moschatus* was described (Ramsay 1876). The Long-nosed Potoroo, *Potorous tridactylus*, was among the first marsupial species encountered by Europeans and was described and figured by both Phillip (1789) and White (1790). Indeed, captive specimens were displayed in London in 1789 (Seebeck 1982a).

Kerr (1792) formally described the Long-nosed Potoroo (as *Didelphis tridactyla*), but the genus *Potorous* was not erected until 1804 (by Desmarest). The specific name refers to the mistaken interpretation of the number of digits on the hind foot. This came about because Kerr apparently did not examine a specimen, but relied on the illustrations published by White (1790). The type no longer exists (Iredale & Troughton 1934). Later descriptions (Cuvier 1798; Shaw 1800) included the Long-nosed Potoroo with the kangaroos and, by implication, indicated that the species was syndactylous. That Desmarest (1804) had examined a specimen seems clear from his recognition of syndactyly.

Although *Bettongia* was not erected until 1837 (by J.E. Gray), two species from opposite ends of the continent, the Tasmanian Bettong, *B. gaimardi*, and the Burrowing Bettong, *B. lesueur*, had been described by French scientists in the early 1820s from specimens collected in 1817 during the voyage of the *Uranie* from the Port Jackson area (Desmarest 1822) and from Dirk Hartog Island (Quoy & Gaimard 1824). Both species are now extinct at their type localities. A third species, the Brush-tailed Bettong, *B. penicillata*, was described by Gray (1837). The Tasmanian Bettong (*B. cuniculus*) was described a year later as a separate species (Ogilby 1838), but was synonymised with *B. gaimardi* in 1967 (Wakefield 1967c). The latter author also described the Northern Bettong, *B. tropica*, and, despite opinions to the contrary (Sharman *et al.* 1980; Christensen 1983) it is recognised as a valid species in this account.

The Rufous Bettong, *Aepyprymnus rufescens*, (as *Bettongia*) was described by Gray (1837), but not recognised as a monotypic genus until 1875 (Garrod 1875).

The Desert Rat-kangaroo (now believed to be extinct), *Caloprymnus campestris* (as *Bettongia*) was described from specimens collected in the ‘interior of South Australia’ (Gould 1843). The modern genus was erected by Thomas (1888).

Although the taxonomic status of some currently recognised subspecies is doubtful (Strahan 1982, 1983), there are 15 described modern forms, nine of which were described between 1837 and 1851. Subsequently, only three species have been recognised: *Hypsiprymnodon moschatus* (Ramsay 1876), *Bettongia tropica* (Wakefield 1967c) and, most recently, the Long-footed Potoroo, *Potorous longipes* (Seebeck & Johnston 1980).

Early discoveries of potoroids were made by French scientific expeditions, notably the voyage of the *Uranie*. Most descriptions, however, came from the extensive collecting by John Gould and his colleagues in the 1840s. Gould's descriptions, illustrations and field observations (Gould 1841–2, 1863) are a landmark in the dissemination of knowledge about Australian mammals and those dealing with potoroids are no exception. For several forms at least, his record is almost all we know about the natural history of the animal. Gould's accounts successfully synthesised his own personal observations, reports from his collectors, aboriginal lore and scientific examination of specimens.

The recognition of the first and subsequent fossil potoroid genera are separated by almost a century. De Vis (1888) described *Propleopus oscillans* (as *Triclis oscillans*) from a single dentary from the Darling Downs in Queensland. This was the only fossil potoroid recognised until Archer (1979) described *Wabularoo*. Recent finds in a number of places in Australia have enabled the rapid recognition of many new genera. This has led to a reappraisal of the family

and the separation of many of these forms into three new subfamilies. Descriptions of *Bulungamaya* and *Gumardee* (Flannery, Archer & Plane 1982) were followed by *Purtia* and *Wakiewakie* (Case 1984; Woodburne 1984b), *Ekaltadeta* (Archer & Flannery 1985) and *Palaeopotorous* (Flannery & Rich 1986). Several other undescribed forms will certainly warrant generic status.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Potoroids have dense fur over all of the body (Fig. 30.1). They have an elongated rostral region, more or less rounded erect ears, large eyes, a long, furred (except in the Musky Rat-kangaroo) tail, the hind limbs longer than forelimbs and very large hind feet. Information on size and weights of the species of Potoroidae is presented in Table 30.1.

The rostral region is variously elongated. In the Broad-faced Potoroo, *Potorous platyops* (now believed to be extinct), the Rufous Bettong and the Desert Rat-kangaroo, it is short and blunt; in the Musky Rat-kangaroo and Long-nosed Potoroo it is long and pointed. The nasal width expressed as a percentage of nasal length may be used as a measure of broadness of face (Table 30.2). In the Desert Rat-kangaroo and the Rufous Bettong this exceeds 60%; in the Broad-faced Potoroo it is 49%, while in the Musky Rat-kangaroo it is only 15%.

The ears in most species are moderately short, rounded and erect and the dorsal base of the ear is generally obscured by head fur. Those of the Desert Rat-kangaroo are proportionally longer and narrower and the base much more evident, enhancing their long narrow appearance.

Table 30.1 Size and weight of modern species of the Potoroidae.

SPECIES	LENGTH (mm) Head & Body Range (mean)	LENGTH (mm) Tail Range (mean)	WEIGHT (g) Range (mean)
<i>Hypsiprymnodon moschatus</i>	153-273 (232)	123-159 (143)	360-680 (530)
<i>Potorous platyops</i>	(243)	(183)	not available
<i>Potorous tridactylus</i>	(360)	198-262 (230)	660-1 640 (1 100)
<i>Potorous longipes</i>	380-415 (400)	315-325 (320)	1 600-2 200 (1 900)
<i>Bettongia lesueur</i>	(370)	(300)	970-1 530 (1 250)
<i>Bettongia penicillata</i>	300-380 (330)	290-360 (310)	1 100-1 600 (1 300)
<i>Bettongia tropica</i>	302-337 (315)	320-335 (328)	not available
<i>Bettongia gaimardi</i>	315-332 (323)	288-345 (326)	1 200-2 250 (1 660)
<i>Caloprymnus campestris</i>	254-280 (268)	297-377 (325)	637-1 060 (889)
<i>Aepyprymnus rufescens</i>	375-390 (385)	338-387 (360)	3 000-3 500 (3 250)

The tail of the Brush-tailed Bettong has a terminal dorsal crest, which has given rise to its common name. In the Musky Rat-kangaroo the tail is clad with small scales rather than fur. Prehensility of the tail is obvious in most *Bettongia* species.

Some fossil forms were markedly larger than animals of modern genera. In *Propleopus chillagoensis*, for example, PM³ is more than twice the length of the same tooth in modern genera. In species of *Ekaltadeta*, *Gumardee* and *Wabularoo*, PM³ is very much larger than all but *Caloprymnus* (Table 30.3, Fig. 30.7).

Body Wall

All potoroids have the normal mammalian integument and are clad with generally short, dense hair over most of the body. The rhinarium is naked in all modern forms. In *Hypsiprymnodon* species the pinnae are mostly hairless and leathery in appearance, but in all others the pinnae are furred to a variable extent. The hair on the lower limbs and feet is very short, as it is on the tail of all but *Hypsiprymnodon*, which is virtually hairless (see above).

Most species are relatively uniform in colour although clines in coat colour may exist in some species. Long-nosed Potoroo populations across northern Tasmania, for example, show coat colour changes from rufous-brown to grey-brown. Generically, coat colour ranges from rich dark chocolate brown (Musky Rat-kangaroo) through browns and greys to rufous (Rufous Bettong) and sandy (some *Bettongia* species and *Caloprymnus* species). Coat colour is usually uniform and unadorned compared with the Macropodidae; no blazes, hip stripes, saddles or ringing are present, although Burrowing Bettongs sometimes have a poorly defined hip stripe (Finlayson 1958; also noted in Tasmanian Bettongs, R.W. Rose unpublished). Musky Rat-kangaroos tend to have a steel-greyish head, but gradation into the chocolate body colour is subtle. The Burrowing Bettong is described as ‘woolly’, the hair being softer than in other species.

The belly fur in most species is pale. The Long-nosed Potoroo exhibits tail-tip albinism which Johnston & Sharman (1976) showed to be clinally related to latitude; albinism is present in 80% of the Tasmanian population and in none of the southeastern Queensland population. Buchmann & Guiler (1974) suggested that the tip might be used in intra-specific signalling, but this seems unlikely considering the inconsistency of its appearance. Tasmanian Bettongs usually have a white tail-tip, as do Burrowing Bettongs. Brush-tailed Bettongs have a black brush tip on the tail. One specimen of a *Caloprymnus* species is known to have had a white tail-tip (Finlayson 1932a).

Lyne (1959) described and figured the vibrissae present in the Tasmanian Bettongs, *Bettongia g. gaimardi* and *B. g. cuniculus*, the Long-nosed Potoroo, and the Desert Rat-kangaroo and provided literature references to vibrissae in the Musky Rat-kangaroo, the Rufous Bettong and the Burrowing Bettong. The Musky Rat-kangaroo differs from all other potoroids in possessing three groups of brachial vibrissae. All groups of facial vibrissae are present in all species examined except for the Desert Rat-kangaroo, in which no interramal vibrissae are present. This species also has a very large number (up to seven pairs) of ulnar carpal vibrissae, compared with between one and four pairs for other species.

Skeletal System

The skull is short, broad and shallow in most modern forms, although in some species of *Potorous* the skull is elongate and narrow (Fig. 30.2). The skull differs from that of the macropodids in several important dental characters, particularly the presence of a well-developed upper canine and a large, plagiaulacoid sectorial premolar (Fig. 30.7). In all potoroids except *Hypsiprymnodon* species, the squamosal bone has wide contact with the frontal bone, unlike macropodids in which parietal/alisphenoid contact is usual.

The mandible is generally elongate and narrow, although in the broader-skulled species (Burrowing Bettong and Desert Rat-kangaroo in particular) it is relatively shortened. The masseteric canal is confluent with the inferior dental canal and extends anteriorly to P3.

The dental formula for *Hypsiprymnodon* is I 3/2 C 1/0 PM 1/1 M 4/4 and for modern Potoroinae is I 3/1 C 1/0 PM 1/1 M 4/4.

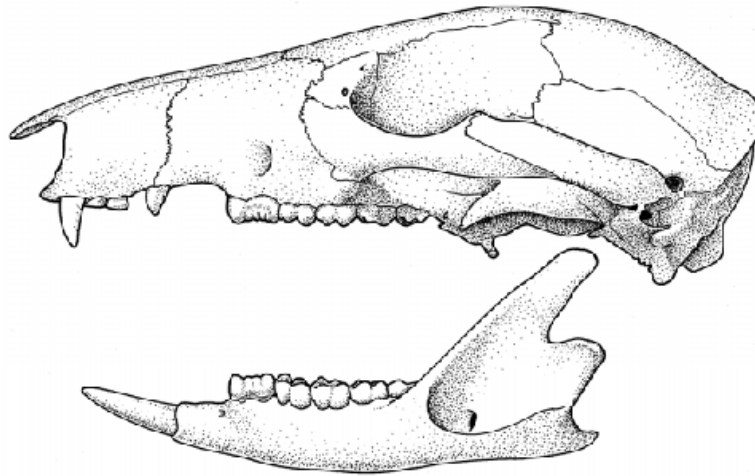


Figure 30.2 Lateral view of the skull of the Long-footed Potoroo (© ABRS)
[G. Milledge]

All young potoroids have two premolars, which are shed near maturity and replaced by a single premolar. This transformation is a good diagnostic feature in determining maturity.

The premolars and molars erupt sequentially and have been used to age potoroids (Tyndale-Biscoe 1968; Christensen 1980a; Rose 1985). There is no forward progression of molar teeth once they have erupted. Subsequent ageing techniques, therefore, must be based on tooth wear. The size of the molars decrease from anterior to posterior. Old animals occasionally develop supernumerary molars that erupt through the bone, but not the cheek membrane (Jones 1924; Rose 1985).

Tooth loss of the pattern seen in macropodids has not been recorded in potoroids and probably is not an important factor in mortality of old animals, although tooth wear may well be.

Parker (1973) described a unique form of 'anisognathy' in Brush-tailed Bettongs, in which the cheek tooth rows cross each other.

The postcranial skeleton in both modern subfamilies is similar. The vertebral column consists of seven cervical, 13 thoracic, six lumbar, two sacral and 22 caudal vertebrae. 13 pairs of ribs are present.

Hypsiprymnodon: Heighway (1939) rightly pointed out that the skull is 'notable for the lightness and delicacy of its structure, and the frailty of the braincase'. The skull is characterised by a long, narrow rostrum. The nasals are long and narrow (see Table 30.2) and the diastema between the canine and first premolar is greater than in any other modern potoroid (in actual as well as proportional dimensions). One lachrymal foramen is present (two in potoroides). The palate shape reflects the dorsal aspect of the rostrum and is long, narrow and pointed. The anterior palatal foramina are long, extending beyond the canines. Large posterior palatal foramina are present, extending anteriorly to about the midline of M². There is no sagittal crest and the occipital crest is weakly developed. The auditory bullae are small and flat (Johnson & Strahan 1982). The mandible is slightly built and relatively shorter than in similarly sized potoroides, more expanded posteriorly and is distinguished by the long diastema between I₁ and PM₁, compared with potoroides. The angular process is short and blunt (Johnson & Strahan 1982).

The dentition of *Hypsiprymnodon* was described in detail by Heighway (1939), Woods (1960a) and Ride (1961). I^1 is the largest of the incisors, but is relatively small compared with that in potoroines. I^2 and I^3 are smaller and similar in structure. The canine is small and peg-like. PM^3 is tall and narrow and is inserted obliquely to the molar row, rotated labially some 20–30°. It is serrate, with a convex occlusal margin which is higher posteriorly. It bears seven nearly vertical ridges. M^{2-4} are quadrituberculate and bunodont. M^5 is triangular in section. The molar gradient is $M^2 = M^3 > M^4 > M^5$. The molar rows are anteriorly divergent.

I_1 is very long, ascending at a low angle. I_2 is minute, tubular and overlaps the base of I_1 (Woods 1960a; Johnson & Strahan 1982). There is no lower canine. PM_3 is similar to PM^3 and, similarly, is inserted obliquely. The molar gradient is $M_2 < M_3 > M_4 > M_5$ and the lower molars closely resemble the upper ones.

The postcranial skeleton was described in detail (and parts illustrated) by Owen (1878), Heighway (1939) and Johnson & Strahan (1982). The skeleton differs from potoroines in that there is less disproportion between the length of the forelimb and that of the hind limb, a situation resembling that in typical possums. The manus is not specialised for digging and the claws function as hooks rather than shovels (Johnson & Strahan 1982).

Table 30.2 Cranial and dental measurements (in mm) and proportions of modern species of the Potoroidae. Abbreviation: BAL = basal length of skull; ZW = zygomatic width; NAL = length of nasals; NAW = width of nasals; LP^3 = length of upper permanent premolar; LM^{2-4} = length of upper molar row M_2 – M_4 ; LTR = length of cheek teeth row to M_4 . Sources: 1, Johnson & Strahan (1982); 2, Thomas (1888) & Smith (1971); 3, Seebeck & Johnston (1980); 4, Finlayson (1958); 5, Wakefield (1967c); 6, Finlayson (1932a); 7, Finlayson (1931).

GENUS/ SPECIES	BAL	ZW	NAL	NAW	LP^3	LP^{2-4}	LTR	ZW/ BAL	LP^3 / BAL	NAL/ BAL	NAW /NAL	SOURCE
<i>Hypsiprymnodon moschatus</i>	51.7	2.6	27.9	4.2	3.9	8.1	12.0	3.1	7.5	4.0	15.1	1
<i>Potorous platyops</i>	50.0	5.0	24.3	11.9	4.8	9.8	14.6	70.0	9.6	48.6	49.0	2
<i>Potorous t. tridactylus</i>	67.7	38.7	34.9	11.5	6.3	11.6	17.9	57.2	9.3	51.6	33.0	3
<i>Potorous t. apicalis</i>	81.8	44.6	34.6	10.6	7.6	13.1	20.7	54.5	9.3	42.3	30.6	3
<i>Potorous longipes</i>	78.8	46.1	36.1	11.3	6.7	13.9	20.6	58.5	8.5	45.8	31.3	3
<i>Bettongia lesueur</i>	60.2	43.5	27.1	12.8	8.4	12.3	20.7	72.3	14.0	45.0	62.2	4
<i>Bettongia penicillata</i>	66.5	42.2	32.5	13.5	7.3	12.4	19.7	63.5	10.7	48.9	41.5	5
<i>Bettongia tropica</i>	64.2	41.2	29.6	13.5	8.3	13.2	21.5	64.2	12.9	46.1	45.6	5
<i>Bettongia g. gaimardi</i>	64.4	42.2	30.8	13.9	7.2	12.8	20.0	65.5	11.2	47.8	45.1	5
<i>Bettongia g. cuniculus</i>	70.6	45.3	34.7	14.5	8.1	13.7	21.8	64.2	11.5	49.2	41.8	5
<i>Caloprymnus campestris</i>	52.6	39.4	27.8	19.3	5.7	12.4	18.1	74.9	10.8	52.9	69.4	6
<i>Aepyprymnus rufescens</i>	72.8	50.5	28.9	18.0	9.5	18.5	28.0	69.4	13.1	39.7	62.3	7

Table 30.3 Teeth of fossil species of the Potoroidae; *maxillary teeth; all others mandibular; n.a. not available. Sources: 8, Archer & Flannery (1985); 9, Woods (1960a); 10, Archer, *et al.* (1978); 11, Case (1984); 12, Flannery *et al.* (1982); 13, Archer (1979); 14, Woodburne (1984b).

GENUS/SPECIES	LP ³ (in mm)	LM ²⁻⁴ (in mm)	NO. OF RIDGES ON P ₃	SOURCE
<i>Ekaltadeta ima</i>	10.7	20.3	6	8
<i>Propleopus oscillans</i>	13.5-15.2	30.1-31.5	6-7	9
<i>Propleopus wellingtonensis</i>	n.a.	29.6	n.a.	8
<i>Propleopus chillagoensis</i> *	21.1	31.3	9	10
<i>Purtia mosaicus</i>	6.6	11.9	8	11
<i>Bulungamaya delicata</i>	6.8	12.2	6	12
<i>Wabularoo naughtoni</i>	10.7-11.2	21.0	8	13
<i>Gumardee pascuali</i> *	10.6	17.8	11	12
<i>Wakiewakie lawsoni</i>	11.0	11.2	20	14

Potorous: The skull in the Long-footed and the Long-nosed Potoroo is elongate and narrow (Table 30.2, Fig. 30.2), but short and broad in the Broad-faced Potoroo. The nasals are long and narrow, except in the Broad-faced Potoroo. The canine is situated midway between I¹ and PM³. The palate is long and narrow, reflecting the elongate rostrum. The anterior palatal foramina are short and terminate anterior to the canines. The posterior palatal foramina are variably short. No sagittal crest is present, but the occipital crest is quite strongly developed. The auditory bullae are small and flat. The mandible is long and slender, the angular process short and blunt. The dentition was described and illustrated by Finlayson (1938), Hope (1969), Smith (1971) and Seebeck & Johnston (1980).

I¹ is large and robust, while I² and I³ are small and similar in appearance. I³ is almost twice as long as I². The canine is well developed and caniniform. PM³ is long and broad, inserted along the axis of the tooth row. It is serrate, with a horizontal or concave occlusal margin. In all species it has three to five vertical ridges, the anterior and posterior being much greater in width than the medial ridges. M²⁻⁵ are quadrituberculate and bunodont. The molar gradient is M³ > M² > M⁴ > M⁵ in the Long-footed Potoroo, and M³ > M⁴ > M² > M⁵ in the Long-nosed and Broad-faced Potoroos, but is not steep in any species. Supernumerary molar teeth may be present. The molar rows are gently curved to follow the shape of the skull and are slightly more divergent anteriorly. I₂ is long and falcate. PM₃ is similar to PM³. The lower molars closely resemble the upper molars and the molar gradient is the same.

Some elements of the postcranial skeleton of the Long-nosed Potoroo were described and illustrated by Merrilees & Porter (1979).

Bettongia: The skull is short and broad, (see Table 30.2), characterised by large posterior palatal foramina, enormously inflated auditory bullae and premolars with more than six vertical ridges. The nasals are short and broad, especially in the Burrowing Bettong. There is a very short diastema between I³ and C¹. The palate is broad, with large posterior foramina (extending to about the junction of M² and M³). Anterior palatal foramina are short in the Brush-tailed Bettong, but longer in other species. A slight crest is developed between the parietals and the inter-parietals and the occipital crest is well-

developed. The mandible is relatively short and deep, especially in Burrowing Bettong. The angular process is long and pointed and the ascending ramus is broad.

Dentition was described and illustrated by Thomas (1888), Finlayson (1958), Wakefield (1967c) and Smith (1971).

I^1 is strong and robust in the Tasmanian Bettong, less so in the other species. I^2 and I^3 are smaller. C^1 is weakly developed and more peg-like than truly caniniform. PM^3 is long and narrow, serrate, with a horizontal or slightly concave occlusal margin. In the Brush-tailed Bettong, it is inserted outwardly oblique to the molar row, but in the other species insertion follows the axis of the molar insertion. In all species it is ornamented with fine vertical ridges (7–8 in the Tasmanian and Brush-tailed Bettongs, 8–9 in the Northern Bettong, and 9–11 in the Burrowing Bettong). The molars are quadrituberculate and bunodont. The molar gradient is $M^3 > M^2 > M^4 > M^5$. Tasmanian Bettongs were reported to develop supernumerary M^6 rarely (Jones 1924). Molar rows are straight or gently curved, but anteriorly divergent in the Tasmanian, Northern and Brush-tailed Bettongs, and decidedly arched in the Burrowing Bettong.

I_2 is long and falcate. PM_3 is similar to PM^3 and lower molars are similar in shape to upper molars, although slightly smaller (Finlayson 1958).

Finlayson (1959) provided measurements of postcranial elements of a single specimen of the Tasmanian Bettong, *Bettongia gaimardi cuniculus*. Some postcranial elements of the Burrowing and Brush-tailed Bettongs were illustrated by Merrilees & Porter (1979) together with distinguishing characters.

Caloprymnus: The skull is very short and broad, with very short, broad and flattened nasals. The nasals crowd out the other premaxillary bones and extend virtually to the edge of the rostrum. Proportionally they are, nevertheless, very long.

Finlayson (1932a) suggested that the presence of an infra-zygomatic process of the maxilla, not found in other potoroids, may be related to diet. The anterior palatal foramina are relatively long, although they do not reach beyond the canine. Posterior palatal foramina are long and reach to M^2/M^3 . Despite the breadth of the rostrum, the palate is relatively narrow. There is a very short diastema between I^3 and C^1 . There are strongly marked temporal ridges, but virtually no occipital crest. The auditory bullae are small and inflated. The mandible resembles those of *Bettongia*, but is shallower. The angular process is short and blunt.

Thomas (1888) and Finlayson (1932a) illustrated and described aspects of the dentition in detail. I^1 is strong and broad; I^2 and I^3 are about the same size although I^2 tends to be wider. C^1 is very small, weak and peg-like. PM^3 resembles that in *Potorous*, with enlarged anterior and posterior ridges. It bears four or five vertical ridges. The occlusal margin is concave.

M^{1-3} are quadrituberculate, M^4 tricuspid; all are bunodont. The molar gradient is $M^2 < M^3 > M^4 > M^5$. The molar row is long, and decidedly arched around the palate. Molar row length (proportionally) is only exceeded by that in *Aepyprymnus*. I_1 is narrow, sharp and falcate. PM_3 resembles PM^3 and lower molars are like the upper molars.

Finlayson (1932a) examined the postcranial skeleton and commented that it resembles other potoroids, although the great length of the hind feet is diagnostic.

Aepyprymnus: This genus is characterised by the absence of posterior palatal foramina (Garrod 1875). Finlayson (1931) pointed out that the skull is very densely ossified and is proportionally much heavier than those of other potoroids. The skull is short and broad (Table 30.2) with a pointed rostrum and a deep, robust zygomatic arch. The anterior palatal foramina are short, terminating well anterior to the canines. A weak sagittal crest is present and a very pronounced occipital crest. The auditory bullae are small and flat. The mandible is relatively short and deep with a short, blunt, angular process.

Finlayson (1931) described and illustrated the dentition. I^1 is almost caniniform, well developed and sharp. I^2 and I^3 are broad, with I^3 almost twice the size of I^2 . It is inserted obliquely to the midline of the tooth row and has a single shallow groove about one-third of the length along its labial surface. The canine is only about the size of M^4 , flattened and sharply tipped. PM^3 is long and broad, inserted in line with the molar row and has seven, eight or nine vertical ridges. The occlusal margin is horizontal or slightly convex, particularly in the unworn state. Molars are quadrituberculate and bunodont, with a tendency towards bilophodonty. The molar gradient is $M^2 < M^3 > M^4 > M^5$ and the molar rows are markedly arched. I^1 is laterally compressed and strong. PM_3 resembles PM^3 in structure, but is decidedly shorter. Lower molars are like the upper ones.

No details of the postcranial skeleton have been reported.

Locomotion

Members of the two living subfamilies exhibit different modes of locomotion.

The Musky Rat-kangaroo is entirely quadrupedal and has both a slow and fast gait. The slow gait resembles that of other macropodoids in that it is synchronously plantigrade, with the main propulsive force coming from a downward movement of the hind limb. The forefeet are placed on the ground, taking the body weight as the hind feet are brought forward and placed outside the forefeet. Unlike all other members of the Macropodoidea, however, the tail is held stretched out, clear of the ground. While the tail does not act as a support, it does act as a body counter-poise, particularly during the fast gait, which is merely a rapid version of the slow gait (Johnson & Strahan 1982).

Slow and fast gaits are also found in the subfamily Potoroinae (Buchmann & Guiler 1974). The slow gait ('quadrupedal crawl') is a pattern followed by *Aepyprymnus*, *Bettongia* and, presumably, *Caloprymnus* and resembles that described for *Hypsiprymnodon*. While the tail drags on the ground (so that tracks include a longitudinal trail), it is not used for support or balance.

The fast gait ('bipedal hop') is characteristic of most macropodoids. It is synchronously digitigrade (but see below, *Caloprymnus*) and also derives its main propulsion from downward extension of the hind limbs. The tail is held horizontally or slightly up-tilted and counterpoises the body. The forelimbs are held backwards and close to the body and only touch the ground when the animal stops, changes direction or mode of travel. *Potorous tridactylus* can travel very rapidly and a speed of 35–36 m/min was reported (Buchmann & Guiler 1974) and may include low leaps of up to 2.5 metres. The pattern for *Aepyprymnus*, *Bettongia* and *Potorous* species is similar, but an examination of tracks left by the Desert Rat-kangaroo (Finlayson 1932a) revealed that the right foot lands some 150 mm in advance of the left and while the right toe is parallel with the direction of travel, the left is rotated some 30° outwards. Aboriginal hunters were well aware of the difference in trails left by the Desert Rat-kangaroo and the sympatric Burrowing Bettong.

The slow gait of animals in both subfamilies is used during leisured foraging, feeding and in other unstressed situations. Females with large pouch-young may use it habitually. The fast gait is used for escape or pursuit.

Climbing has been observed in *Potorous* and *Bettongia* species (Buchmann & Guiler 1974; Krefft 1862; Seebeck 1982a). Krefft reported that captive Brush-tailed Bettongs often escaped from an 'enclosure of pine logs about seven feet (2.3 m) high, which they used to climb with a nimbleness truly astonishing ...'. Musky Rat-kangaroos have been observed to climb about fallen logs and low branches and captive specimens have been reported to climb slim (50 mm diameter) branches at angles of up to 45° and to 'show no hesitation when moving above the ground' (Johnson & Strahan 1982; Johnson, Haffenden & Denison 1983).

Flannery, Archer & Plane (1984) postulated that the extinct propleopids were quadrupedal rather than saltatory (like the *Hypsiprymnodontinae*), viewing quadrupedal locomotion as the ancestral mode of movement in macropodoids.

A variation of locomotion is involved in the use of the tail in the transport of nest-building material by several species of the Potoroinae, especially *Bettongia*. Stodart (1966b) reported the Burrowing Bettong collected nesting material in its mouth before transferring it via the forefeet and hind feet to the prehensile tail (Fig. 30.1). Rufous Bettongs carry only a fraction of the material carried by the smaller, but proportionately longer-tailed *Bettongia* species (Viola 1977). Prehensility, although obvious by behaviour, is not apparent in the tail structure of either the Burrowing Bettong or the Rufous Bettong. Long-footed and Long-nosed Potoroos also transport nesting material using the tail.

Feeding and Digestive System

Perhaps for convenience, Hume (1982) grouped the rat-kangaroos under the heading of 'Herbivorous Marsupials', believing that most species had a diet of mainly non-fibrous plant material. More recently, Lee & Cockburn (1985) considered that most potoroids should be categorised as fungivore/omnivores, since many species eat a diet high in hypogean (underground) fungi and may be opportunistic insectivores or even scavengers. Burrowing Bettongs have been observed to eat dead fish on the shore line (Ride & Tyndale-Biscoe 1962). An exception may be the Musky Rat-kangaroo, which has been classified as a frugivore/omnivore (Johnson & Strahan 1982; Lee & Cockburn 1985).

Potoroids have well-developed claws on their forelimbs, which they use to dig for food. Sampson (1971), Parker (1973) and Rose (1985) described how *Bettongia* species occasionally bury and store seed which are eaten later, often after germination had begun.

The inner 'kernel' of fungi eaten by Brush-tailed Bettongs contains up to 10% protein, 42% lipid and less than 1% ash. The protein is deficient in certain amino acids, but it is believed that gut micro-organisms can redress this imbalance (Kinnear *et al.* 1979; Frappell & Rose 1986). Guiler (1971b) studied the diet of the Long-nosed Potoroo in Tasmania between May and December. Although there are seasonal variations in food taken, fungi forms the major part of the diet (67–92%).

Sampson (1971) described Brush-tailed Bettongs chewing seeds and spitting out the 'epidermal material and hard parts'. He further described the sucking-out of the soft parts of insects and the subsequent egestion of the exoskeleton. This would account for the common finding that potoroid faeces contain little hard or recognisable material. During feeding in this bettong (a 'rapid feeder'), the mandibular incisors are pressed against or pushed into soft food while the maxillary teeth steady it. The blade-like premolars are used on harder food. Since the molar teeth decrease in size posteriorly from the premolars, maximum

forces should operate near the premolars (Parker 1973). One individual Long-nosed Potoroo was observed to excavate 26 fungi in less than 20 minutes (O. Buchmann, personal communication). Rapid feeding may be an anti-predator adaptation.

The structure of the stomach of most potoroids was described by Langer (1980) and reviewed by Hume (1982). There are fewer descriptions of the whole digestive tract, although Heighway (1939) described this in detail for the Musky Rat-kangaroo and Carr (1970) and Frappell (1984) provided details of the digestive system of the Long-nosed Potoroo (Fig. 30.3). The digestive system of potoroids is characterised by a very large sacciform forestomach, little development of the tubiform forestomach with only limited sacculation, a small hind stomach and the presence of a ventricular groove along the lesser curvature of the stomach (Hume 1978, 1982). In the Rufous Bettong the tubiform forestomach is absent. The potoroid hind gut exhibits a well-developed, though simple, caecum and proximal colon (Hume 1978).

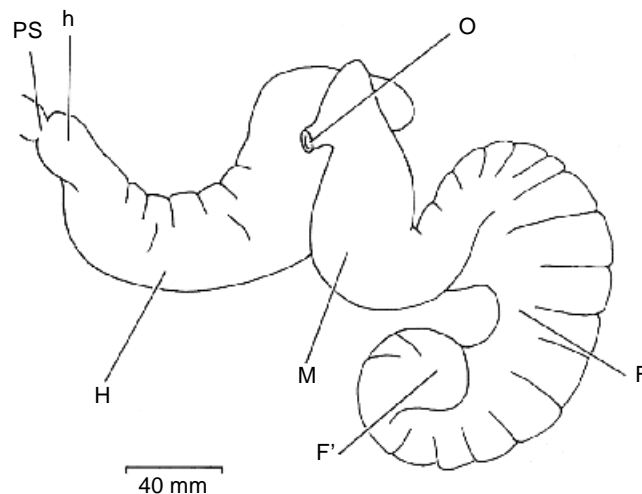


Figure 30.3 Diagrammatic view of the stomach of an adult Long-nosed Potoroo viewed from the ventral side. **F**, sacciform forestomach; **F'**, sacciform forestomach tip; **M**, tubiform forestomach; **H**, hindstomach; **h**, pylorus; **O**, oesophagus; **PS**, pyloric sphincter. (After Frappell, 1984; © ABRS) [B. Scott]

The forestomach in potoroids is lined with cardiac glandular epithelium, there being no areas of squamous epithelium (Langer 1980). The hind stomach contains cardiac, fundic and pyloric mucosa.

The functional implications of the structure of the potoroid digestive system are not obvious. Hume (1978) believed that the larger sacciform forestomach may have evolved as a storage organ as well as a fermentation region. A storage organ would allow these relatively small marsupials to avoid predators by actively feeding for only short periods. A fermentation region would provide foregut digestion of cellulose such as occurs in ruminants and in many macropodids. Potoroid foregut fermentation (Carr 1970; Kinnear *et al.* 1979; Hume & Carlisle 1985) may have evolved to correct the nutritional imbalance caused by a fungivorous diet. Fungi are deficient in several essential amino acids, but microbial intervention can overcome this problem. Further digestion, perhaps including that of cellulose, may take place in the caecum (Frappell & Rose 1986).

Circulatory System

Although there is little specific information available, the circulatory system appears to be typical of most mammals. The structure of the heart of the Musky Rat-kangaroo has been briefly described by Heighway (1939) and is similar to that of other marsupials. However, the auricular appendage of the right atrium is 'large and folded around the aorta rather than bifurcating to enclose it'. There are slight differences in the way in which major blood vessels arise from the base of the aorta in the Tasmanian Bettong and the Long-nosed Potoroo (Pearson 1940), but this probably has little functional significance. There is a vascular plexus between the ovary and uterus on either side in the Long-nosed Potoroo; Shaw & Rose (1979) speculated that this may mediate local hormone effects between these two organs. A testicular rete mirabile composed of an intermingling of both testicular arteries and veins is present in most marsupials, including the Potoroidae. This rete seems likely to be involved in cooling the blood coursing towards the testis. Barnett & Brazenor (1958) reported that the Long-nosed Potoroo, in relation to body size, had the lowest number of rete vessels of all marsupial species. Bryant & Rose (1985), however, have recently shown that this potoroo has a normal complement of vessels (25 arteries and 25 veins).

Parsons *et al.* (1971); Parsons, Guiler & Heddle (1971) and Ward, Green & Rupp (1974) provided much haematological detail for the Long-nosed Potoroo. The data from the former study suffer from the fact that wide ranges are given for most measurements, while the latter study examined anaesthetised animals and reports no unusual findings in the haematological values. From the relationship between the heart rate and weight for marsupials (Kinneir & Brown 1967), one would expect most potoroids to have rates from 80–100 beats/min.

Respiration

Heighway (1939) provided a very brief description of the trachea and lungs in the Musky Rat-kangaroo. Both lungs are trilobate; the right organ has a well-markedazygous lobe. The tidal volume of the Long-nosed Potoroo is approximately 5 ml at thermoneutrality and the respiratory minute volume is less than 0.5 L/min (Nicol & Maskrey 1977). Hudson & Dawson (1975) reported that the respiratory rate of Long-nosed Potoroos is 30–40 breaths/min and that oxygen consumption is approximately 0.45 ml/g/h, similar to that found by Nicol (1976). Oxygen consumption in the larger Tasmanian Bettongs is 0.42 ml/g/h (Rose 1987a), a value that increases by 24% when a large pouch-young is present. Calculations of basal metabolic rates from the oxygen consumption data show that both Long-nosed Potoroos and Tasmanian Bettongs have metabolic rates rather higher than the norm for marsupials.

The resting body temperature (T_b) of mainland Long-nosed Potoroos is 35.9°C (Hudson & Dawson 1975), while at similar ambient temperatures, that of the Tasmanian Long-nosed Potoroos T_b is 36.8°C (Nicol 1978a). The higher T_b of the Tasmanian form could be due to their insulation, as Hudson & Dawson (1975) noted that a Tasmanian/mainland hybrid has a thicker coat than do mainland animals. The T_b of Tasmanian Bettongs varies over a 24 hour period. It is at its lowest at midday ($T_b = 36.2^\circ\text{C}$) when the animal is asleep and reaches a maximum near midnight ($T_b = 37.5^\circ\text{C}$) when it is active (Rose 1985). In females of this species, the minimum daily T_b or basal body temperature varies during the oestrous cycle (Rose 1985).

At low ambient temperatures, Long-nosed Potoroos maintain their T_b by shivering and an increase in oxygen consumption (Nicol 1976, 1978a). Well-constructed nests probably also assist in the maintenance of T_b during inactive periods for some potoroids. Long-nosed Potoroos respond to

increases in ambient temperature by an increase in evaporative water loss (Hudson & Dawson 1975; Nicol & Maskrey 1977). Respiratory rates increase up to tenfold at high ambient temperatures. At very high ambient temperatures water loss from dense rings of sweat glands at the base of the tail exceeded the total respiratory water loss. The highest rates of sweating, in excess of 600 g/m²/h were higher than in most eutherians (Hudson & Dawson 1975). The Red Kangaroo, *Macropus rufus*, is the only other macropodoid reported to use sweating as an evaporative cooling device (Dawson, Robertshaw & Taylor 1974).

There are few studies on the temperature-regulating abilities of the other potoroids. In dry environments, Brush-tailed Bettongs increase their evaporative water loss at ambient temperatures above 30°C (Sampson 1971). Both Brush-tailed and Tasmanian Bettongs alter the degree of insulation provided by their nests depending on temperature. After being chased, Tasmanian Bettongs sweat from the base of the tail (R.W. Rose, unpublished data).

Excretion

There is very little information on the structure and function of the potoroid kidney or its ability to produce urine. Heighway (1939) gave some general anatomical details of the kidney, ureters, bladder and urethra in the Musky Rat-kangaroo, but did not note any departure from the usual mammalian pattern. The Brush-tailed Bettong has a low turnover of water in summer, which increases with the availability of water. Summer water requirement per day is approximately 50 ml. Higher levels of water turnover in winter may be due to a higher metabolic rate (to cope with heat loss) or to the fact that more water is ingested with food.

Because it is able to live for years in areas of Western Australia which have no free water and apparently does not visit water holes during drought periods, the Brush-tailed Bettong is believed to rarely drink free water in the wild (Sampson 1971). This species appears able to extract sufficient water from its diet and is able to restrict water loss. The Long-nosed Potoroo has a daily water turnover of 150 ml, similar to that of the Red Kangaroo, but greater than the Tammar Wallaby, based on standardised weight (Denny & Dawson 1975). The total body water of the Long-nosed Potoroo is 59% of body weight, slightly less than that of the larger macropodids, but similar to that found for bandicoots (Hulbert & Dawson 1974a).

Sense Organs and Nervous System

Heighway (1939) described the external appearance of the brain of the Musky Rat-kangaroo and states that 'taken as a whole the brain did not diverge markedly from the diprotodont plan'. The brain has the characteristic arched shape of macropodoids, and includes the 'paramedial' sulcus which Heighway (1939) believed to be a distinctive feature of 'Macropodids'.

Johnson (1977) and Haight & Murray (1981) depicted the external morphology of the brain of potoroids. The brain to body-mass ratio was greater in the Long-nosed Potoroo than in two macropodids examined and, in fact, was greater than most other marsupials. Haight & Murray (1981) contrasted the macropodids, in which there is a tendency towards the reduction of olfactory structures, with the potoroids, in which olfactory structures are more prominent.

Dillon (1963a) concluded that, on the basis of the structure of the neocortex, the Long-nosed Potoroo was the most primitive of six species of kangaroo examined. The corticospinal fibres in this potoroo extend as far as level T12, further than in any other marsupial studied (Martin, Megirian & Connor 1972).

Sanderson, Haight & Pettigrew (1984) described the dorsal lateral geniculate nucleus and its retinal projections. The cyto-architecture of the Tasmanian Bettong nucleus is relatively simple compared to other macropodoids; in contrast, the lateral geniculate nucleus of the Long-nosed Potoroo is quite complex. Both species display the same basic pattern of retinal termination.

The structure and function of the pineal gland of the Long-nosed Potoroo differ little from that described for other marsupials (Bradley 1973). Varying light regimes have no effect on the pineal gland in males.

A vomeronasal organ is present. In the Rufous Bettong it opens anteriorly, directly into the nasal cavity, as in murids and lagomorphs (Russell 1985). Though not proven, this sensory area may be involved in the perception by males of sexually responsive females. Johnson (1980) described the importance of sniffing and marking in the social behaviour in this species.

Endocrine and Exocrine Systems

While the mean total serum thyroxine level ($1.86 \pm 0.83 \mu\text{g}/100 \text{ ml}$) of Long-nosed Potoroos is low, the effective level of thyroxine is similar to that of Tammar Wallabys and most eutherians. ACTH and cortisol have no noticeable effect on carbohydrate or nitrogen metabolism of potoroids. Injection of insulin ($0.2 \text{ i.u.}/\text{kg}$) into Long-nosed Potoroos results in a decrease in plasma glucose that returns to normal values within three hours; cortisol ($5 \text{ mg}/\text{kg}/\text{d}$ for 5 days) treated animals showed virtually the same response (A. Bradley, personal communication).

Long-nosed Potoroos exhibit a typically mammalian response to the injection of adrenalin (Nicol 1978a). Plasma glucose levels double and oxygen consumption and the release of free fatty acids increase. Plasma glucose levels in handled Tasmanian Bettongs are higher than in any other macropodoid (A. Bradley & R.W. Rose, unpublished data). Most researchers of potoroids would be well aware of the 'nervousness' of their animals and the care needed to be applied in all physiological experiments in order to minimise stress. The sweat glands surrounding the base of the tail of Long-nosed Potoroos respond to intradermal injections of adrenalin (Hudson & Dawson 1975).

The sweat glands of the Long-nosed Potoroo have no direct innervation, a characteristic of animals in which sweating is not a primary thermoregulatory mechanism (Manolis & Dawson 1980). In addition to the concentrated rings of sweat glands around the tail and, to a lesser extent, the lower parts of the hind limbs, sweat glands are found inside the pouch of the Tasmanian Bettong (S.A. Dick & R.W. Rose unpublished data). The white oily secretion of the paracloacal glands may be used in scent marking of territories in *Bettongia* species (Christensen 1980a).

The mammary gland is similar in structure (H.M. Crowley & R.W. Rose, unpublished data) and function in potoroids to that found in other marsupials. The gland dramatically increases in size in late lactation, reaching a peak at the time of final pouch vacation, and there is a corresponding lengthening of the teat. An oxytocin injection leads to milk ejection in potoroids, as in other marsupials.

Substantial changes in the composition of the milk of Long-nosed Potoroos and Tasmanian Bettongs occur throughout lactation (Rose 1987a). For much of pouch life, milk carbohydrate is high ($10 \text{ g}/100 \text{ ml}$) and lipid low ($1\text{--}2 \text{ g}/100 \text{ ml}$), but protein increases gradually to $4\text{--}8 \text{ g}/100 \text{ ml}$. Milk solid levels gradually become more concentrated, reaching 50% at weaning. There are dramatic changes in milk composition at pouch-young emergence as carbohydrate levels fall sharply to $3 \text{ g}/100 \text{ ml}$, lipid values rise to $14 \text{ g}/100 \text{ ml}$ and protein continues to rise to levels of $10\text{--}13 \text{ g}/100 \text{ ml}$. The energy content of the milk increases throughout lactation, beyond pouch life and into the weaning period, concomitant with the increase in lipid levels.

Reproduction

The karyotypes of potoroids are summarised in Table 30.4. Despite morphological similarity, the two species of *Potorous* have quite different chromosome numbers and sex-determining mechanisms.

Rodger (1978) gave a detailed review of male potoroid reproductive organ structure. As in most marsupials, the paired testes are prepenial and scrotal. The prostate gland is carrot-shaped as in macropodids and there are three pairs of Cowper's or bulbo-urethral glands (Owen 1841). Potoroids, as in macropodids but unlike many other marsupials, have an undivided glans penis.

Table 30.4 Chromosome number and sex chromosomes in Potoroidae. Sources: Sharman (1961a); Hayman & Martin (1969); Seebeck & Johnston (1980).

SPECIES	2N	SEX CHROMOSOME
<i>Hypsiprymmodon moschatus</i>	22	XY/XX
<i>Potorous tridactylus</i>	13 ♂ 12 ♀	XY ¹ Y ² /XX
<i>Potorous longipes</i>	24	XY/XX
<i>Bettongia lesueur</i>	22	XY/XX
<i>Bettongia gaimardi</i>	22	XY/XX
<i>Bettongia penicillata</i>	22	XY/XX
<i>Aepyprymnus rufescens</i>	32	XY/XX

The penis is held retracted by the cremaster muscle and is extruded through the urogenital (cloacal) aperture prior to mating. Hughes (1964) and Cleland (personal communication to Rodger 1978) gave details of the spermatozoal morphology of potoroids. Rodger (1978) stated that the spermatozoa of potoroids are indistinguishable from those of macropodids.

As potoroids are able to breed throughout the year, the males are always in reproductive condition (Hughes 1964; Sampson 1971; Rose 1985).

There are few experimental studies of male potoroid reproduction. Cadmium was found to destroy spermatogenesis in the testes of Long-nosed Potoroos (Bryant & Rose 1985). These authors (unpublished data) have also shown that the degenerative changes that occur in testes which had been relocated in the abdomen were similar to those reported in other marsupials and eutherians.

The anatomy of the female reproductive tract of most members of the Potoroidae was described by Pearson (1944a, 1944b, 1945) (Fig. 30.4). As in all marsupials there are paired ovaries, uteri and lateral vaginae. The potoroids differ from most macropodids in the presence of an anterior vaginal expansion or caecum. In addition, both the Burrowing Bettong (Tyndale-Biscoe 1968) and the Rufous Bettong (Moors 1975) possess an anterior vaginal cul-de-sac. In all potoroids the median vagina or birth canal is transient, only formed near the time of birth and then quickly degenerates (Rose 1978). Flynn (1922); Hughes (1962a, 1962b) and Bryant & Rose (1986) commented on the presence of more than one apparently active corpus luteum in the ovary of the Long-nosed Potoroo. This is unusual, since all potoroids except the Musky Rat-kangaroo produce but a single young. Some Long-nosed Potoroo ovaries contain polyovular follicles (Ullmann & Brown 1983), although Hughes (1962a) stated that only single ovulation occurs.

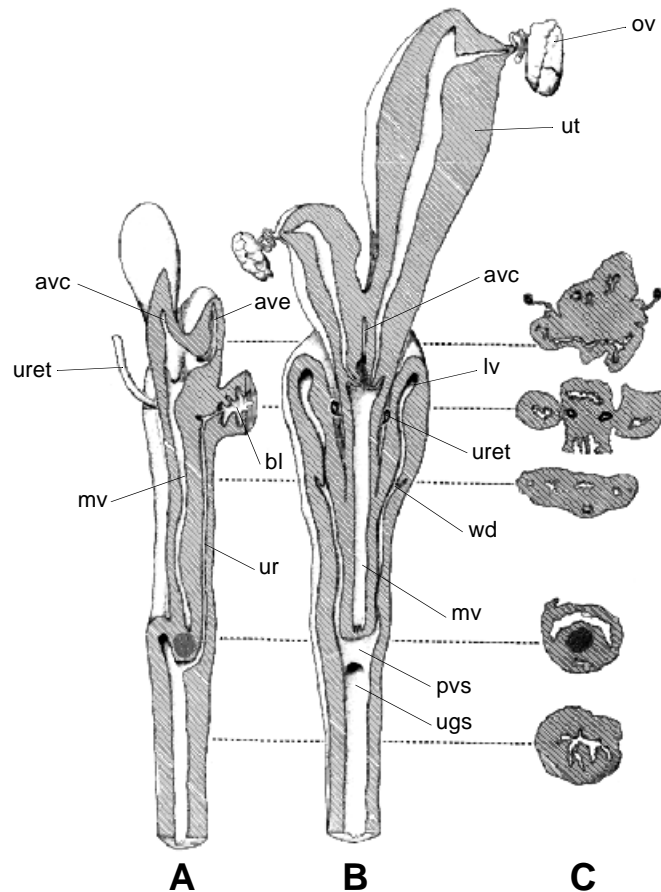


Figure 30.4 Female reproductive system of the Tasmanian Bettong. **A**, Lateral longitudinal section; **B**, ventral longitudinal section; **C**, transverse sections at various levels. avc = anterior vaginal cul-de-sac; ave = anterior vaginal expansion; bl = bladder; lv = lateral vagina; mv = median vagina; ov = ovary; pvs = posterior vaginal sinus; ugs = urogenital sinus; ur = urethra; uter = ureter; ut = uterus; wd = Wolffian duct. (After Tyndale-Biscoe, 1968; © ABRS) [B. Scott]

Reproductive behaviour is basically similar in all species. Males regularly inspect the pouch and external cloacal region of most females, though should this activity continue for too long, unresponsive females lie on their side and lash out with their hind feet. On the day of oestrus there is much following around as males and females hop about in unison. Males mount from behind and grasp the females' thorax with their forelimbs and perhaps bite or hold on with their teeth. Mating is rarely prolonged, lasting usually only for a few minutes at a time, but may occur several times on the one night. Mating only occurs on the night of oestrus in Tasmanian Bettongs (Rose 1985), but Hughes (1962a) reported that female Long-nosed Potoroo may receive the male on many occasions, in one instance over a 12 day period. Excited males may move their tails in a laterally sinuous movement.

The reproductive life histories of the Potoroidae are compiled in Table 30.5. The table is based on numerous studies, summarised in Rose (1978) and Lee & Cockburn (1985). Potoroids are able to breed throughout the year in captivity, though in the wild there may be some restrictions, perhaps due to harsher environmental pressures.

Table 30.5 Some parameters of reproduction in the family Potoroidae. (Data from Rose, 1987b; Tyndale-Biscoe, 1968; Parker, 1977 & personal communication; Hughes, 1962a; Shaw & Rose, 1979; Moors, 1975; Johnson, 1979). *Pouch life of *Hypsiprymnodon* is 147 days (Johnson & Strahan, 1982) and for *Potorous longipes* 140-150 days (Seebeck, 1982).

	<i>Potorous tridactylus</i>	<i>Bettongia lesueur</i>	<i>Bettongia penicillata</i>	<i>Bettongia gaimardi</i>	<i>Aepyprymnus rufescens</i>
Oestrous cycle length (days)	42	22.2	22-23	22.6	21-25
Gestation length (days)	38	21.3	21	21.3	21-23.6
Delayed gestation length (days)	29	20	21	18	18.7
Average pouch life (days)*	126	115	100	106	114

Cyclic variation in the cellular constituents of the vaginal smear occurs in potoroids (Hughes 1962a; Tyndale-Biscoe 1968; Rose 1987b). In general, oestrus is associated with a dramatic rise in cornified epithelial cells (often comprising 80% of the smear) and a concomitant decrease in leucocytes. Even higher levels of cornified cells are present for several days after oestrus. During the post-oestrous period, leucocytes and non-nucleated epithelial cells predominate, but their proportions vary erratically. Particularly in association with the presence of sperm, the sudden increase in cornified cells and marked decline in leucocytes is a very useful indicator of oestrus.

On the basis of histological changes in the ovary and uterus, the oestrous cycle can be subdivided into follicular and luteal phases. This can be quantified by measuring the time from removal of the active corpus luteum to oestrus (= follicular phase) and subtracting this value from the length of the oestrous cycle. The luteal phase of the oestrous cycle of the Long-nosed Potoroo is 18 days (Shaw & Rose 1979; Bryant & Rose 1985) and that of the Tasmanian Bettong 15 days (Rose 1987b).

The gestation length of most potoroids is given in Table 30.5. The family includes both the shortest gestation length (21 days: all *Bettongia* species) and the longest (38 days: Long-nosed Potoroo) of all Macropodoidea. As with many macropodids, the gestation period is only a little shorter in duration than the oestrous cycle, so that birth is followed almost immediately (often on the same night) by a 'post-partum' oestrus during which the female may mate. Should pregnancy occur, the fertilised egg of this second mating remains quiescent or dormant during most of the period when the pouch is occupied. When the pouch young is removed, lost or nears the end of pouch life, the quiescent blastocyst becomes activated and development continues to term. This delayed gestation is shorter than the undelayed gestation by 2-3 days, but in the Long-nosed Potoroo, it is shorter by as much as 9 days (Shaw & Rose 1979). The fact that embryonic quiescence or diapause occurs in all the Potoroinae and the Macropodidae (the condition in the Hypsiprymnodontinae is unknown) is strong evidence that it also occurred in the common ancestor of both the Potoroidae and the Macropodidae (Rose 1978). Whatever the selection pressures for the evolution of diapause might have been, diapause functions to prevent successive young occupying the pouch simultaneously, to allow the rapid replacement of young lost from the pouch and, to effect an almost immediate replacement of young leaving the pouch naturally (Rose 1986b).

Shaw & Rose (1979) and Rose (1985), following Flynn (1930), described the changes in the reproductive tract during pregnancy in Long-nosed Potoroos and Tasmanian Bettongs, respectively. In both species, the corpus luteum found at ovulation initially results in stimulation of both uteri, but after 4–5 days, the uterine glands on the same side as the ovary containing the corpus luteum are significantly more stimulated than their opposite. This occurs whether or not the mother becomes pregnant and may be due to facilitated transport of progesterone (from the corpus luteum) via the vascular plexus in the region (Shaw & Rose 1979). Later in pregnancy, however, the feto-placental unit itself has a role in stimulating the pregnant uterus as this stimulation is absent in non-pregnant females. This stimulation, over and above that of the corpus luteum, allows potoroids to continue their pregnancies past the luteal phase and into the follicular phase in such a way that birth occurs shortly before oestrus and its subsequent ovulation. This phenomenon also occurs in many macropodids and presumably results, in general, in better developed and larger young than in marsupials with shorter gestations (Sharman 1965; Rose 1978). The presence of the fetus has other effects on the mother, usually grouped under the heading ‘maternal recognition of pregnancy’. The oestrous cycles of Tasmanian Bettongs containing a pregnancy are shorter by 1.5 days than those cycles of non-pregnant animals. The pouch tightens dramatically with the imminent birth of a new young and the large furred young always vacates the pouch as a result (Rose 1986b, 1987b).

In the Long-nosed Potoroo, removal of the corpus luteum before day six of a delayed pregnancy (that is, a pregnancy due to reactivation by the quiescent blastocyst following removal of a pouch young) inhibits embryonic development. From 6–21 days after removal of a pouch young, the removal of the corpus luteum does not prevent embryos developing to full term, but interferes with birth. Removal of the corpus luteum on day 25 after removal of a pouch young allows birth, but impairs subsequent lactation. By day 27 of this 29 day delayed gestation, the corpus luteum no longer appears to be essential for embryonic development, birth or neonatal survival in the pouch. The corpus luteum may be required for a slightly greater proportion of pregnancy than in most macropodids because the birth canal in potoroids is transient and must be prepared before each parturition (Bryant & Rose 1985).

Most potoroids are mature by the age of 1 year, though maturity in Long-footed Potoroo males may take as long as 2 years (Seebeck 1982b). Most potoroids have a high reproductive potential as they mature early compared to the macropodids, are able to breed continuously, have a short pouch life that allows approximately three young per year and live for 5 or more years.

Embryology and Development

Kerr (1934, 1936) described in some detail the early development of the Tasmanian Bettong, *Bettongia gaimardi* (as *B. cuniculus*). Other authors provided further prenatal details for the Tasmanian Bettong (Flynn 1930; Rose 1985) and the Long-nosed Potoroo (Hughes *et al.* 1978; Shaw & Rose 1979) (Table 30.6).

After birth, development continues in the pouch for a period of 4–5 months (Table 30.5). During much of this period, growth rates vary between potoroid species, but Rose (1985) showed that their growth rate is twice as fast as that in macropodids (Maynes 1976; Rose 1985, 1987a).

Table 30.6 Embryonic development of the Long-nosed Potoroo and the Tasmanian Bettong. RPY = removal of pouch young. Data from Hughes *et al.* (1978), Rose (1985) and Shaw & Rose (1979).

<i>Bettongia</i>		<i>Potorous</i>		STAGE
DAYS AFTER RPY	SIZE (mm)	DAYS AFTER RPY	SIZE (mm)	
0	0.26	0	0.23	unilaminar blastocyst
3	0.26	2	0.25	unilaminar blastocyst
		6	0.56	bilaminar blastocyst
5	1.1	10.5	1.4	bilaminar blastocyst
7	2.5	14	2.2	medullary plate
11	7.5	21	7.0	early fetus
17	14.0	28	15.5	near-term fetus

In the Tasmanian Bettong, head length increases linearly as in most potoroids, but tail and pes length increase in a sigmoidal fashion. Rapid growth in the pes occurs midway through pouch life so that by pouch vacation potoroids have the characteristically long feet of all macropodoids. Growth rates decline after emergence from the pouch even though the absolute growth (grams/day) increases for a period. Rose (1987b) suggested that the decline is due, in part, to a partitioning of maternal milk from growth towards maturation and thermoregulatory functions. Growth in the wild may be less rapid than in captivity (Taylor & Rose 1987). At pouch vacation, young are approximately 20% of their mother's weight; adult weight and maturity are usually attained within 1 year.

Details on growth are available for most potoroides: Long-nosed Potoroo (Guiler 1960a); Long-footed Potoroo (Seebeck 1982b); Brush-tailed Bettong (Sampson 1971; Christensen 1980a); Burrowing Bettong (Tyndale-Biscoe 1968); Tasmanian Bettong (Rose 1985); and Rufous Bettong (Johnson 1980). Data for the Musky Rat-kangaroo are not available. As the young grow in the pouch, they pass through various developmental stages as described by Guiler (1960a) for the Long-nosed Potoroo and by Rose (1985) for the Tasmanian Bettong. A summary of these changes is included in Figure 30.5.

NATURAL HISTORY

Life History

Potoroids are relatively long-lived, with life spans of more than 7 years in the wild and up to 12 years in captivity (Guiler & Kitchener 1967; Collins 1973; Seebeck 1982a; Johnston 1983). Sampson (1971) considered that both sexes of the Brush-tailed Bettong are relatively long-lived and that the population suffers consistent losses of animals of different ages.

Sexual maturity may be reached as early as 6 months [Rufous Bettong (Schlager 1981); Burrowing Bettong (Tyndale-Biscoe 1968)] or as late as 2 years [Long-footed Potoroo (Seebeck 1982b)]. Females of most species produce their first offspring when about 1 year of age (Guiler 1960b; Hughes 1964; Parker 1973; Johnson & Strahan 1982; Seebeck 1982a). Potoroids are non-seasonally polyoestrus as breeding is continuous. A female may produce 10–15 young

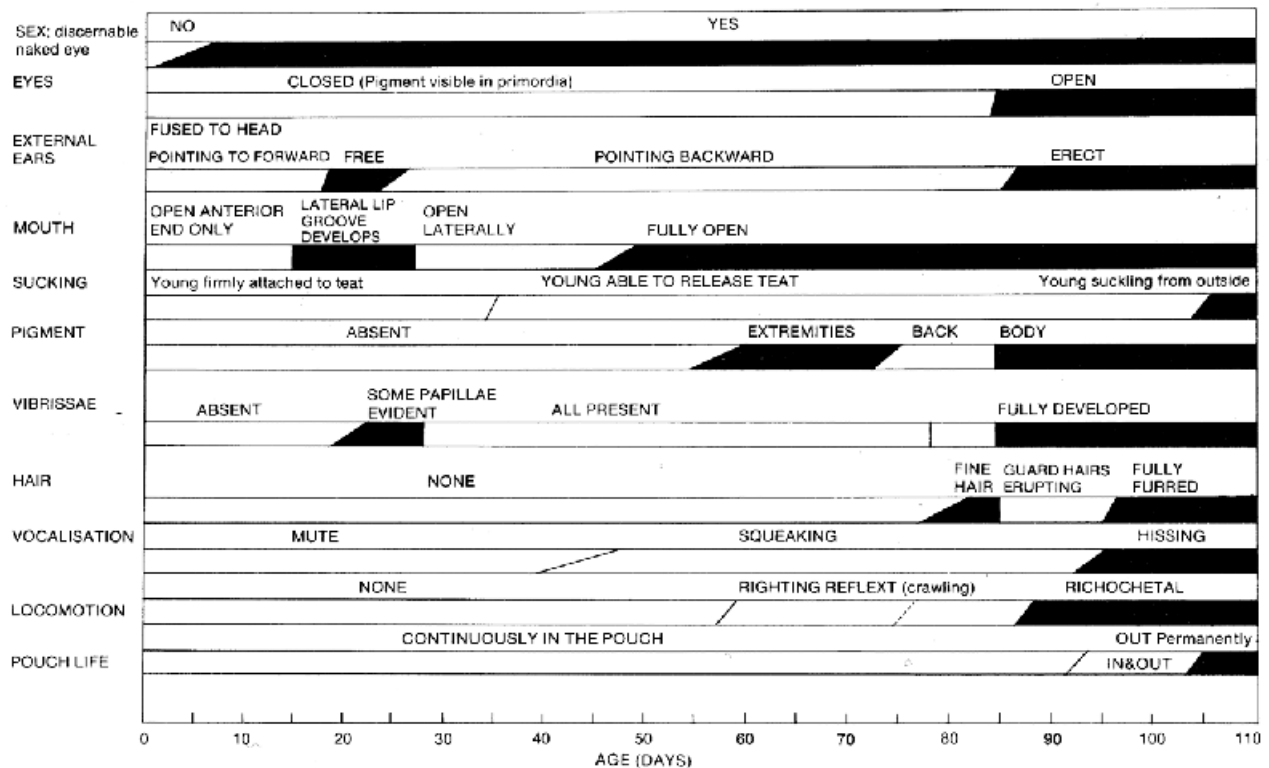


Figure 30.5 Developmental changes in young Tasmanian Bettongs. (After Rose, 1985)

during her lifetime, though only one is born at a time except in the Musky Rat-kangaroo (Kitchener 1967; Sampson 1971; Bennett 1984, 1986). Twins have been observed in Long-nosed Potoroos (S. Johnston personal communication).

Ecology

Although all modern potoroids are omnivores, there is increasing evidence that many species are, to a large degree, mycophagous. *Potorous* and *Bettongia* species are certainly in this category (Kitchener 1967; Guiler 1971b; Christensen 1980a; Drinnan & Hill 1984; Hill & Triggs 1985; Rose 1986a), whereas Rufous Bettongs (Schlager 1981) eat fungi throughout the year, although remaining primarily rhizophagous. At times, however, fungi do become the predominant food item of this species. Vegetable matter other than fungi is the dominant food of the Musky Rat-kangaroo, which feeds on tuberous roots (Ramsay 1876) and a variety of rainforest fruits (Johnson & Strahan 1982). Soil and litter invertebrates form a part of the diet of all potoroids (Christensen 1980a; Drinnan & Hill 1984; Guiler 1971b; Hill & Triggs 1985; Johnson & Strahan 1982; Kitchener 1967; Ramsay 1876; Sampson 1971; Schlager 1981), and Burrowing Bettongs have also been observed eating carrion (Ride & Tyndale-Biscoe 1962).

Potoroids do not seem to drink water, although Finlayson (1931) believed that the Rufous Bettong does not cope well during drought and provides evidence of the animals' search for water in dried up stream-beds. Schlager (1981), however, did not believe that the species requires much, if any, free water. Dahl (1926) did not observe Burrowing Bettongs drinking water although ample supplies were present. Main & Yadav (1971) determined that the species' daily water intake was only 3% of body weight and that the species also has renal adaptations to conserve water.

The Musky Rat-kangaroo is found only in rainforest, where fruits and invertebrates are readily available (Johnson & Strahan 1982). Both extant species of *Potorous* are found in forested areas, but the Long-nosed Potoroo in particular displays a wide ecological tolerance (Calaby 1966; Kitchener 1967; Heinsohn 1968; Emison *et al.* 1978; Schlager 1981; Seebeck 1981b; Amos 1982; Menkhorst & Beardsell 1982). Whatever the floristic or precise structural form of its habitat, this potoroo appears to need a dense cover at ground level through which it forms and utilises a system of known runways. It does not usually venture more than a few metres from this cover to feed (Guiler 1958; Kitchener 1967; Heinsohn 1968; Seebeck & Johnston 1980; Seebeck 1981b; Chesterfield *et al.* 1983; Drinnan & Hill 1984; Horrocks *et al.* 1984; Opie *et al.* 1984; Hill & Triggs 1985). The only information available on habitat for the now extinct Broad-faced Potoroo, *Potorous platyops*, is 'thicket surrounding one of the salt lagoons' (Kitchener 1983c).

Whereas *Potorous* species prefer dense cover, *Bettongia* species are found in much more open habitat. *Bettongia* formerly occurred over a very wide range of arid and semi-arid habitats in Australia (Dahl 1926; Kershaw 1952; Finlayson 1958; Ride & Tyndale-Biscoe 1962; Main & Yadav 1971; Sampson 1971; Green 1974; Christensen 1980a; Christensen & Leftwich 1980; Rose 1986a).

Of all the Potoroidae, the Desert Rat-kangaroo, *Caloprymnus campestris* inhabited the most arid habitat. Finlayson (1932a) described the habitat of this species as stony flats, transitional between gibber plains and loamy flats, supporting sparse shrubs and very scattered clumps of *Hakea* species.

Aepyprymnus rufescens, the Rufous Bettong, requires habitat similar to that of *Bettongia* species, but has a preference for open, grassy woodland and forest. Schlager (1981) described the habitat as having no shrub-layer, only tall native grasses.

The distribution of some potoroids may be dictated by their low-fibre diet, which may affect their utilisation of some habitats (I.D. Hume personal communication). The very widespread distribution of the Potoroidae, especially in the southern part of the continent, raises some queries about the validity of Hume's suggestion.

Potoroids are generally solitary animals, whose pair-groupings are usually brief encounters during mating and longer associations between mother and young-at-heel. Occasionally, animals feed in loose aggregations. Johnson & Strahan (1982) reported as many as three Musky Rat-kangaroo individuals feeding together on fallen fruit and several Rufous Bettongs have been observed feeding in pasture (Schlager 1981). Seebeck (unpublished data) has also observed several Long-nosed Potoroos feeding in loose aggregations. Heinsohn (1968) considered that the lack of scars on wild Long-nosed Potoroos indicates a lack of aggressive behaviour. Dempster (1965) stated that these potoroos rarely fight in captivity. Kitchener (1967) established an artificial feeding site for this species and observed that the aggression between individuals incorporated a dominance hierarchy, perhaps because the dominant animal (a female) had the feeding site within her home range. Schlager (1981) found no evidence of territoriality in Rufous Bettongs. Christensen (1980a) and Christensen & Leftwich (1980) found that Brush-tailed Bettongs defend only the nest area.

There seems to be little interspecific interaction, most species of Potoroidae appearing undisturbed by encounters with other native or introduced non-predators (Kitchener 1967; Schlager 1981). Rufous Bettongs and rabbits may compete for some food resources (Schlager 1981).

The area of the home range has been determined for only a few species. Long-nosed Potoroo individuals in Tasmania have quite large overlapping home ranges of about 5–20 ha (Kitchener 1973a). Males have significantly larger ranges than females. Seebeck (unpublished data) and Bennett (1986), however,

found that the home range of Long-nosed Potoroos in southwestern Victoria was much smaller, Seebeck recording 1.9 ha for males, 1.4 ha for females and Bennett 2.0 ha for males and 1.5 ha for females. Male home ranges may overlap several females' home ranges, but female home ranges are often exclusive. Preliminary indications are that Long-footed Potoroos have home ranges exceeding 10 ha (Hill & Triggs 1985). Sampson (1971) and Christensen (1980a) reported home ranges of 20–35 ha for Brush-tailed Bettongs. Rufous Bettongs have loosely overlapping home ranges of about 20 ha (Schlager 1981). Potoroids living in dense vegetation seem to require much smaller home ranges than those of more open habitats, despite an equivalence in the animals' size and an overlap in dietary requirements.

Russell (1984) summarised the pattern of social organisation for Long-nosed Potoroos, and Burrowing and Rufous Bettongs. The variables she considered are: social unit, unit of dispersion of population, spacing pattern, mating system, pattern of parental care, dispersal of young and reproductive pattern. The patterns are generally the same for all species. Burrowing Bettongs in captivity have a harem structure (one male and several females), but this may not be so in the wild. The young of the three species disperse at or near weaning. Perhaps because of the lack of field data, Russell (1984) concluded that spacing of the social unit (which means home range exclusivity) varies; little or none of the home range of Rufous Bettongs or Long-nosed Potoroos is exclusive, whereas part of the home ranges of Burrowing Bettongs and Tasmanian Bettongs are exclusive. The Long-nosed Potoroo does, however, seem to have a small core area which is exclusive (Bennett 1986; Seebeck, unpublished data) and perhaps the same is true for the Rufous Bettong. All except the Burrowing Bettong are generally promiscuous. Parental care is Russell's Type III; permanent attachment of a pouch-young to the teat is followed by intermittent attachment until its eyes are open and its body is well furred. After emergence of the young from the pouch, the young follows the mother until weaning, at which stage it disperses. There is a close coordination of mother-young behaviour, most evident in sucking, pouch entry and exit and in following. Young are responsible for maintaining proximity to the parent and weaning is usually due to lack of cooperation by the mother (Russell 1982).

Predation is a potential regulator of populations for all potoroids because of the animals' size and generally terrestrial behaviour. Native and introduced carnivorous mammals, owls (especially the Masked Owl, *Tyto novaehollandiae*), Wedge-tailed Eagle, *Aquila audax*, Osprey, *Pandion haliaetus*, varanid lizards, and pythons are all predators of *Potorous* and *Bettongia* species (Dahl 1926; Finlayson 1958; Ride & Tyndale-Biscoe 1962; Kitchener 1967; Heinsohn 1968; Seebeck 1978; Christensen 1980a, 1980b; Schlager 1981; Drinnan & Hill 1984; Rose 1986a). Long-nosed Potoroos in Tasmania are thought to avoid most of its potential predators by selecting dense habitat; foxes are not present in that State. Drinnan & Hill (1984) and Hill & Triggs (1985) considered that foxes and dingoes are important regulators of the population densities of the Long-footed Potoroo. Christensen (1980a, 1980b) reported that predation of Brush-tailed Bettongs by foxes and western quolls (*Dasyurus geoffroyi*) is increased by the removal of shelter cover by fire.

Roberts (1970) and Collins (1973) listed the following genera of ectoparasites, mainly fleas, ticks, mites and lice, on various potoroids::

Hypsiprymnodon: *Mesolaelaps* and *Trichosurolaelaps* species (Acarina);

Potorous: *Acanthopsylla* and *Pygiopsylla* species (Siphonaptera); *Amblyomma*, *Haemaphysalis* and *Ixodes* species (Acarina);

Bettongia: *Ceratophyllus*, *Echidnophaga*, *Pygiopsylla* and *Stephanocircus* species (Siphonaptera); *Australaelaps*, *Haemaphysalis* and *Ixodes* species (Acarina); *Heterodoxus* species (Phthiraptera);

Aepyprymnus: *Ctenocephalides* and *Ctenocephalus* species (Siphonaptera); *Haemolaelaps*, *Haemaphysalis* and *Ixodes* species (Acarina); *Boopis* and *Paraheterodoxus* species (Phthiraptera).

Endoparasitic cestodes and nematodes have been reported in the Rufous Bettong (Schlager 1981) and *Potorous* species (Johnston & Mawson 1949; Collins 1973; Spratt & Varughese 1975).

Protozoan blood parasites have been recorded in *Bettongia* and *Potorous* species (Collins 1973). Long-nosed Potoroos are prone to pneumonia in captivity (Guiler 1971a). Seebeck (1982a) reported no specific problems with disease in captive Long-nosed Potoroos but one aged captive Long-footed Potoroo died from bronchopneumonia.

Behaviour

Russell (1982, 1984) reviewed aspects of parental care and social behaviour, notably communication and reproductive behaviour. The latter, and behaviour concerned with home range establishment and feeding have already been addressed.

Potoroids communicate in several ways, but vocalisation is restricted. Female Rufous Bettongs use a soft grunt to call pouch young. Long-nosed Potoroos utter a 'kiss-kiss' sound for the same purpose and when distressed. Distress in Rufous Bettongs is signalled by hissing and in Burrowing Bettongs by grunting. Sexually stimulated vocalisation in this species is a rapid 'thk-thk-thk' sound made by males (Stodart 1966b). A low volume growl is made by female Rufous Bettongs when approached by males. The volume increases as oestrus approaches. Subordinate males utter high-pitched growling when harassed by a dominant male (Johnson 1980). Burrowing Bettongs produce a noisy exhalation in time with hopping (Stodart 1966b). Musky Rat-kangaroos are reported to produce only a short cough (Johnson & Strahan 1982) and the Desert Rat-kangaroo a harsh aspirate sound similar to other marsupials (Finlayson 1932a).

Erect threat postures are common to most marsupials, including potoroids, and are often accompanied by vocalisation (Russell 1984). Rufous Bettongs stamp the hind feet as a danger signal. Sinuous lateral tail movement may serve as a sexual signal or indicate distress or nervousness, depending on the situation. Rufous Bettongs use their tail during urine/cloacal gland marking (Johnson 1980).

Tactile communication is usually observed only between females and young and during courtship, when males will attempt to restrain females by grasping the flanks with their forearms. Aggressive interactions between males or females may involve fighting, with animals lying on their sides and lashing out with their hind feet (Stodart 1966b). Musky Rat-kangaroo males and females also will stand erect face-to-face and mutually touch heads and necks with forepaws. Allogrooming (either female-male or female-female) has been reported for Rufous Bettongs and Burrowing Bettongs.

Self-grooming is typically kangaroo-like. Licked forepaws and/or tongue are used for the head, limbs, torso and tail, the syndactylous toes of the hind feet for accessible parts of the body and the forepaws for the flanks and posterior body. Captive Burrowing Bettongs groom whilst in their shelters rather than in the open (Stodart 1966b).

Potoroids have, as do other marsupials, extensive areas of olfactory receptor cells and the olfactory lobes of the brain are prominent. The well-developed vomeronasal organ may be a specialised receptor for pheromones. Scent glands are certainly present in the mouth region. Paracloacal glands also occur (Russell 1984) and are used in marking (Johnson 1980).

The Musky Rat-kangaroo differs from the other family members in being completely diurnal. It sleeps by night and in the middle of the day rests in a leaf and fern nest. Most activity occurs in the early morning and late afternoon (Johnson & Strahan 1982).

The Long-nosed Potoroo is partly diurnal and may be active during the latter part of the day when the sky is overcast and ambient temperatures are low (J.H. Seebeck unpublished data). All other potoroids are nocturnal, emerging at dusk or later. Most activity occurs early in the night, followed by a rest period (Stodart 1966b; Christensen & Leftwich 1980). Rufous Bettongs build nests before retiring well before sunrise (Johnson 1980). Rain and wind depress activity of, or unsettle, captive Rufous Bettongs and Burrowing Bettongs, but no such trends were observed in a wild population of Long-nosed Potoroos (J.H. Seebeck unpublished data).

The learning capacity of potoroids in the wild has not been formally studied, but certainly the forest species such as the Long-nosed Potoroo incorporate learned runways and trails within their home ranges. In captivity, these potoroos quickly develop particular pathways in the enclosures and this trait may be used to regularly capture the animals for examination (Seebeck 1982a).

Economic Significance

Agricultural Importance: Brush-tailed, Burrowing and Rufous Bettongs were considered significant agricultural pests during the early years of settlement. Delroy *et al.* (1986) quoted a plaintive letter in *Farm & Garden* in 1859 from a farmer troubled by 'these destructive creatures. Shooting is too slow and expensive, sulphur is of no mortal use, drowning is useless, burning chaff is no better, and poison I dare not'. His 'problem' was the Brush-tailed Bettong. Jones (1924) also reported how, because of the destruction of garden produce, the same species was exterminated on St Francis Island, South Australia, by specially imported cats.

Gould (1863) said of the Burrowing Bettong: 'It is one of the most destructive animals to the garden of the settler that occurs in Western Australia, almost every kind of vegetable being attacked by it, but especially peas and beans'. Finlayson (1958) reported that these animals were abundant north of Adelaide in 1855–56, where they damaged standing crops and hay stacks. In 4 nights, 149 animals were shot, including 50 in 1 night. Jones (1924) recorded that in times of stress these bettongs became 'extremely bold, and will enter a homestead in their search for anything to eat'. Poisoned pollard was used to exterminate them in the north of South Australia. Lyne (1974a) reported that 'the Boodie occupied pride of place on the farmers' list of pests in the wheatlands, and were destroyed in huge numbers – 400 being poisoned in one 12 ha paddock'. Brush-tailed Bettongs were used for coursing, being sold by the dozen for ninepence per head in Adelaide around 1900 (Jones 1924).

Even more of a perceived agricultural pest was the Rufous Bettong. They were 'in plague proportions' in northeastern New South Wales in the 1880s and 1890s (Cameron 1975). Bounties were paid by local pasture protection boards. Armidale Pasture Protection Board offered, in 1887, a bounty of threepence per scalp, which rose to sixpence in 1890, then dropped to twopence between 1902 and 1913, when the bounty was stopped. Johnson & Jarman (1975) presented a graph of scalp returns showing that about 163 000 bounties were paid between 1900 and 1913. Schlager (1981) reported that Tamworth Pasture Protection Board paid bounties on 78 938 scalps in 1897 alone. Cameron (1975) reported that Tenterfield Pasture Protection Board paid 11 264 bounties in 1889 and 16 429 in 1892.

The Armidale Pasture Protection Board discontinued the bounty in June 1913 because the species was considered to have declined and to be falling prey to foxes. Johnson & Jarman (1975) considered this probably correct, but that the final disappearance of tussock grassland under grazing pressure and pasture improvement was also important. Those authors did 'not know where we could find rat-kangaroos on the Tablelands now'.

The Rufous Bettong was also a pest to farmers in Queensland. They were 'cordially detested' by cotton farmers in the Callide Valley south of Rockhampton and, therefore, were poisoned. 'Scores of thousands have been killed ... and skeletons are littered thickly around the cotton plots' (Finlayson 1931).

The Long-nosed Potoroo was accused of damaging potato crops (Lydekker 1894). It was also hunted for sale as game (Wheelwright 1861).

Today, only Rufous Bettongs remain in sufficient numbers to be of any concern at all to agriculturalists. As McCann (1975) pointed out, its small size and low numbers make its impact on crops (particularly lucerne) insignificant.

Medical Importance: The Long-nosed Potoroo has few, large chromosomes ($2n=12$ female, $2n=13$ male), all of which are readily distinguishable from each other (Sharman & Barber 1952). Tissue cultures derived from this species have been used in cytological research (Bates *et al.* 1972; Walen & Brown 1962).

Scientific Importance and Conservation Legislation: All species are of intrinsic scientific importance, the more so since most taxa are either extinct, threatened or vulnerable. Conservation of all remaining forms is thus a prime consideration in all States and Territories where they occur. All are protected under State or Federal Wildlife Protection Acts and special reserves have been proclaimed for certain species.

Despite its endangered rating at both State (Ahern 1982) and Federal level (Burbidge & Jenkins 1984), the Long-footed Potoroo is not specifically catered for in the reserve system. Forest management planning, however, is directed at maintenance of the species throughout its known range. The three known populations of Brush-tailed Bettongs in Western Australia are all in reserves. Each of the islands to which it has been reintroduced or introduced in South Australia are strict conservation reserves.

The Tasmanian Bettong is considered to be vulnerable in Tasmania because only 5% of its habitat is within conservation reserves. Over the remainder of its range, forestry operations are altering habitat and hence reducing populations (Rose 1986a). The Long-nosed Potoroo in Tasmania is probably less threatened because its preferred habitat is less likely to be altered during forestry operations and it is known (Hope 1969; Johnston 1973; Seebeck 1981b) to be able to survive in small isolates of gully vegetation, at least in the short term.

Schlager (1981) provided suggested guidelines for the conservation of the Rufous Bettong in New South Wales. Sampson (1971) and Christensen (1980a), similarly, have developed management plans for the Brush-tailed Bettong in Western Australia. The Desert Rat-kangaroo has not been collected since 1932.

Study Techniques: In addition to live-trapping, modern studies involve radiotelemetry, through the use of small transmitters usually fitted to the animal with a collar. Both Sampson (1971) and Christensen (1980a) studied habitat selection and ranging in Brush-tailed Bettongs by this means. Hill & Triggs (1985) and Scotts & Seebeck (1988) used the technique to examine similar parameters in Long-footed Potoroos. Johnson, Catling & Newsome (in Schlager 1981) and Schlager (1981), respectively, have tested and/or used radiotelemetry to study the Tasmanian Bettong in Tasmania and the Long-nosed Potoroo and Rufous Bettong in New South Wales. In other methods, Schlager (1981) followed Rufous Bettongs to which he had attached plastic collars individually

marked with reflective tape and Scotts & Seebeck (1988) used fine thread running out from a spool attached to Long-footed Potoroos to follow released animals' routes.

Newsome, McIlroy & Catling (1975) prepared soil plots to record footprints of vertebrates including Long-nosed Potoroos in south-eastern New South Wales during an assessment of wildlife changes after fire.

Since the development of criteria for reliable identification of the hair of Australian mammals (Brunner & Coman 1974), much use has been made of carnivore scat analysis in surveying the presence of small mammals in particular areas, or of the possible effects of the predator(s) on small mammal populations. Seebeck (1978) investigated fox predation of the Long-nosed Potoroo. Similarly, Schlager (1981) assessed fox and dingo predation on Rufous Bettong and Long-nosed Potoroo populations. Hill & Triggs (1985) and Scotts & Craig (1988) have used scat analysis as a specific survey tool for determining the distribution of Long-footed Potoroos. The latter authors have also developed a hair sampling tube for the same purpose.

Predictive modelling using BIOCLIM (Busby 1985) was applied by Scotts & Seebeck (1988) to determine likely areas in which to search for the Long-footed Potoroo in eastern Victoria and south-eastern New South Wales.

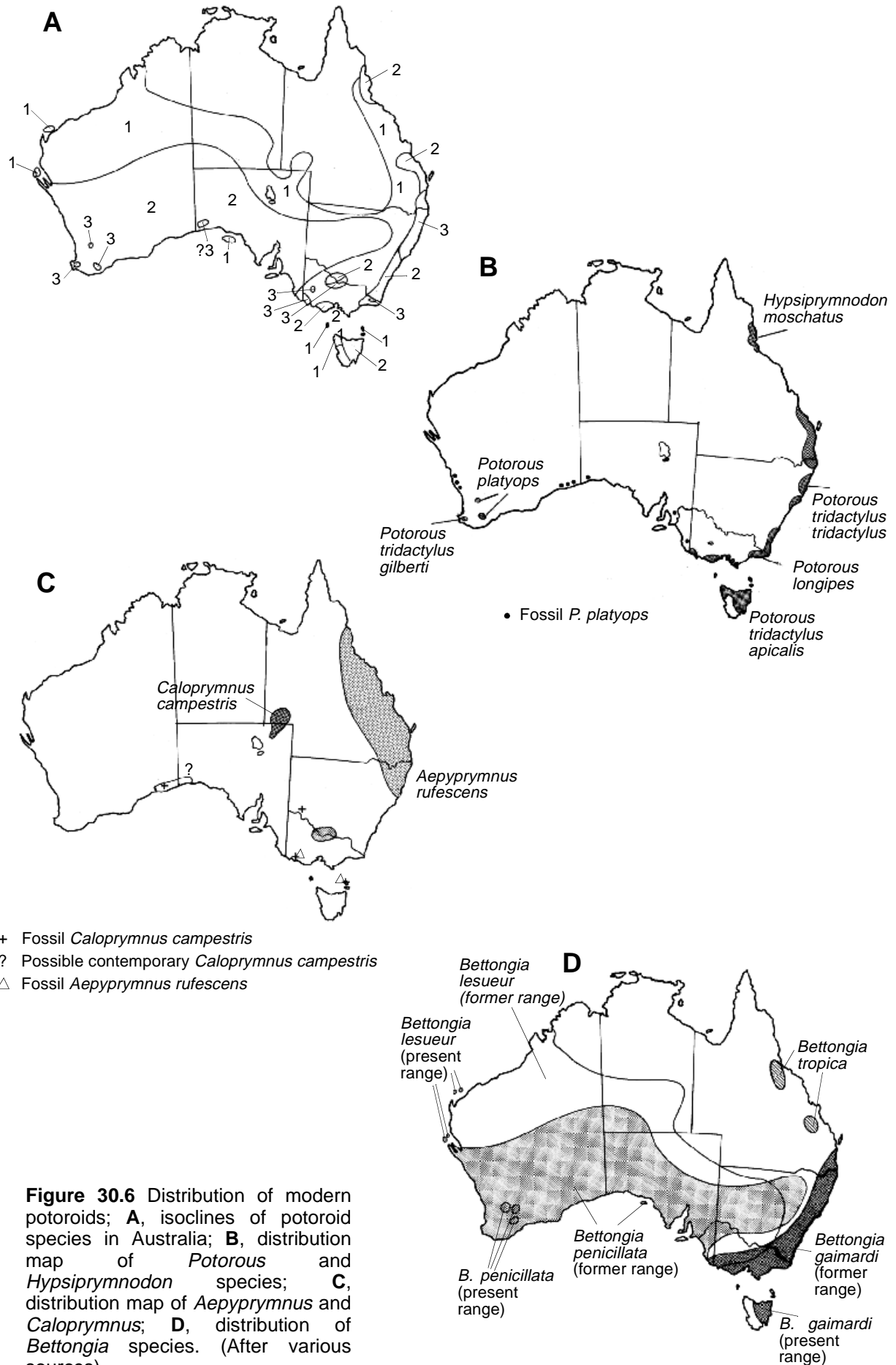
Management Practices: Most management of potoroids, especially of the Burrowing Bettong and the Brush-tailed Bettong, is based on protection within conservation reserves. Brush-tailed Bettongs have been studied in detail by Sampson (1971) and Christensen (1980a) who developed plans for habitat management based on the frequency of controlled fire in the reserves. Sampson (1971) suggested: at Tuttanning the maintenance of floral diversity to provide shelter and food plants requires a 10–15 year burning cycle; that overgrazing by the Western Grey Kangaroo, *Macropus fuliginosus*, needs to be controlled; and that uncontrolled wildfire be excluded. These measures could, together with proper management of the other two reserves for Brush-tailed Bettongs, ensure the continued survival of this species. In contrast, Christensen (1980a) believed that Brush-tailed Bettongs are well adapted to fire, or is indeed 'fire dependent', in that food and cover vegetation species on which it depends are adapted to specific fire regimes. Exclusion of hot fire could therefore eventually eliminate the species from the particular habitat. Christensen (1980b) implicated foxes in the decline of the Brush-tailed Bettong and stated that during management for maintenance of the species, the control of fox populations will be essential.

Schlager (1981) also implicated foxes in the decline of the Rufous Bettong in north-eastern New South Wales and recommended control of foxes by aerial baiting. He also recommended monitoring and control of rabbits and hares both of which compete with this bettong for food, refuge sites and by increasing predator densities. The species can benefit from some aspects of low-intensity agriculture and forestry but such practices need to be carefully monitored. Management of land for the Long-nosed Potoroo in northeastern New South Wales is related to the provision of suitably dense cover and control of increased predator pressure.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Before European settlement, modern potoroids were distributed very widely throughout the southern half of the continent (Fig. 30.6A). With the exception of the Musky Rat-kangaroo and the Northern Bettong in northern Queensland, most species were confined to below about 20°S.



Relatively few islands (apart from Tasmania) supported potoroids, but some islands have been of great conservation value for Burrowing Bettongs (Fig. 30.6D). Most habitats within the general range were occupied by at least one species, although normally not more than three.

The arid and semi-arid parts of the continent supported four species, including those with the widest continental range (Burrowing and Brush-tailed Bettongs), while the temperate/tropical east and south-east supported six species. Victoria, with a combination of Bassian and Eyrean habitats had six species, as did Queensland (Bassian, Eyrean and Torresian).

Several species (two tropical, one temperate and two semi-arid/arid) seem always to have had restricted distributions, so that only five species were widespread and apparently common.

Changes caused by European activity – stock introduction, clearing, agriculture, introduction of predators/competitors and hunting caused a very rapid decline in the range of many species, especially those in the more arid parts of Australia. Two species are probably extinct and three are restricted to small remnants of their former range.

Only the Rufous Bettong (Fig. 30.6C) and the Long-nosed Potoroo (Fig. 30.6B) remain relatively widespread and common within their former range. The Tasmanian Bettong (Fig. 30.6D) is common in Tasmania, although extinct on the mainland.

Affinities with other Groups

Pearson (1945) demonstrated that the plan of the female urogenital system of the rat-kangaroos was homogeneous and different from all other diprotodontids; the group was thus monophyletic. He regarded them as a highly specialised offshoot from primitive phalangers, placing them in a separate family, the Potoroidae. In a later paper, Pearson (1950) enlarged upon this theme, incorporating other evidence, and presented a phylogeny which clearly demonstrated the common ancestry and relationships between potoroids and macropodids. He divided the Potoroidae into the subfamilies *Hypsiprymnodontinae* and *Potoroinae*.

Other workers, however, did not support the family Potoroidae nor the separation into two subfamilies (Woods 1960a). Kirsch (1968, 1977a) retained the older concept, as did Bartholomai (1972), Kirsch & Calaby (1977), Marshall (1981b) and Honacki, Kinman & Koepl (1982). Archer & Bartholomai (1978), however, reinstated Pearson's familial standing for the Potoroidae. This was reinforced by Archer (1981b) who presented a phylogenetic tree for the family. Subsequent workers in Australia (Flannery 1982, 1984a, 1984b; Flannery *et al.* 1982, 1984; Johnson & Strahan 1982; Strahan 1983; Poole 1984) recognised the familial status of the Potoroidae. Case (1984) argued that the older view, as defined by Marshall (1981b), should prevail thus reducing the extent of the family as espoused by Flannery (1984a, 1984b), but Flannery *et al.* (1984) rejected Case's arguments.

The phylogenetic relationships of the Potoroidae and its sister family, the Macropodidae, are better documented than most other groups. Ride (1978) reviewed much of the earlier research and this was updated by Archer (1984b) and Flannery (1984a). Most authors have treated the kangaroos as a single family, the Macropodidae, comprising three subfamilies, one of which was the Potoroinae (including *Hypsiprymnodon*). Phylogenetic studies of macropodid origins have thus encompassed the origins and relationships of the rat-kangaroos and as this is documented in the Chapter on the Macropodidae, we will not consider it in detail.

We consider that there are two separate, albeit closely related, families: the Potoroidae and the Macropodidae within a single superfamily and that the two families have been separated for some 57 million years (Air *et al.* 1975). This date, which is based on studies of amino acid sequences and assumptions of constant rates of change, awaits corroboration from as yet undiscovered fossil material (there are no Australian marsupial fossils of such antiquity). Although the Phalangerioidea (excluding the Vombatoidea) are the closest apparent relatives of Macropodoidea (Kirsch 1977a), on the basis of the retention of different premolar teeth, they did not give rise to the Macropodoidea (Archer 1984b). Both groups may have a common ancestor for which no fossils have yet been discovered. In many of Australia's oldest fossil deposits both potoroids and macropodids are present, although potoroids, while out-numbering macropodids in species diversity, do not do so in numbers.

Several alternatives have been offered to explain the relationship between the potoroids and macropodids. The views that potoroids are descendants of macropodids or that potoroids gave rise to the macropodids were discounted by Archer (1984b). The concept that potoroids had a diphyletic origin, *Hypsiprymnodon* and *Bettongia* arising from one group of possums and *Potorous* and *Caloprymnus* from another, with this latter potoroid group giving rise to macropodids (Bensley 1903), was also refuted by Archer (1984b). That author did accept that the potoroid/macropodid common ancestor would have to be a potoroid if a new taxon were not to be erected.

Hume (1978, 1982) suggested that macropodids may have arisen at the same time as eutherian foregut fermenters (that is, in the Late Oligocene–Early Miocene), when grasses first appeared and that browsing macropodids descended from potoroids. Langer (1980), on the basis of the stomach structure, believed that the two groups have a common ancestor.

Potoroids differ from macropodids in a number of cranial characters, the most important being: I^2 and I^3 are smaller than I^1 and more laterally placed; C^1 is well developed (it is absent in most genera of macropodids and where present, is rudimentary); presence of a very large sectorial premolar (Fig. 30.7); molars are relatively low-crowned; the diastema is shorter. In modern forms, at least, they also differ in external characters. Modern potoroids are smaller (*Aepyprymnus*, the largest, weighs up to 3.5 kg) and have small, rounded ears in contrast to the large, pointed ears of most macropodids.

Relationships within the Potoroidae

Archer (1984b) constructed a cladogram showing how he believed all potoroids (past and present) to be related. It gives little information about the relationships of extant potoroids except that *Hypsiprymnodon* is separated from all others. Most authors accepted this division and went further to state that *Hypsiprymnodon* is the least specialised potoroid (reviewed by Johnson & Strahan 1982). It seems likely that the Musky Rat-kangaroo shared a common ancestor with the Potoroinae. Within the latter there have been few attempts to place the extant species in any phylogenetic framework. Pearson's (1945) view of the family interrelationships has been corroborated to some extent by studies on chromosome number (Sharman 1961a) and serology (Kirsch 1977a). These studies have shown that *Bettongia* and *Aepyprymnus* are more closely related to each other than either is to *Potorous*. The position of *Caloprymnus* is more difficult to determine, but on the basis of dentition and reproductive tract, it may be closer to *Potorous* than to the other genera.

Several species exist today in *Potorous* and in *Bettongia*, although there have been some recent extinctions. On appearance, the Long-footed and Long-nosed Potoroos are obviously related, but their karyotypes are quite different.

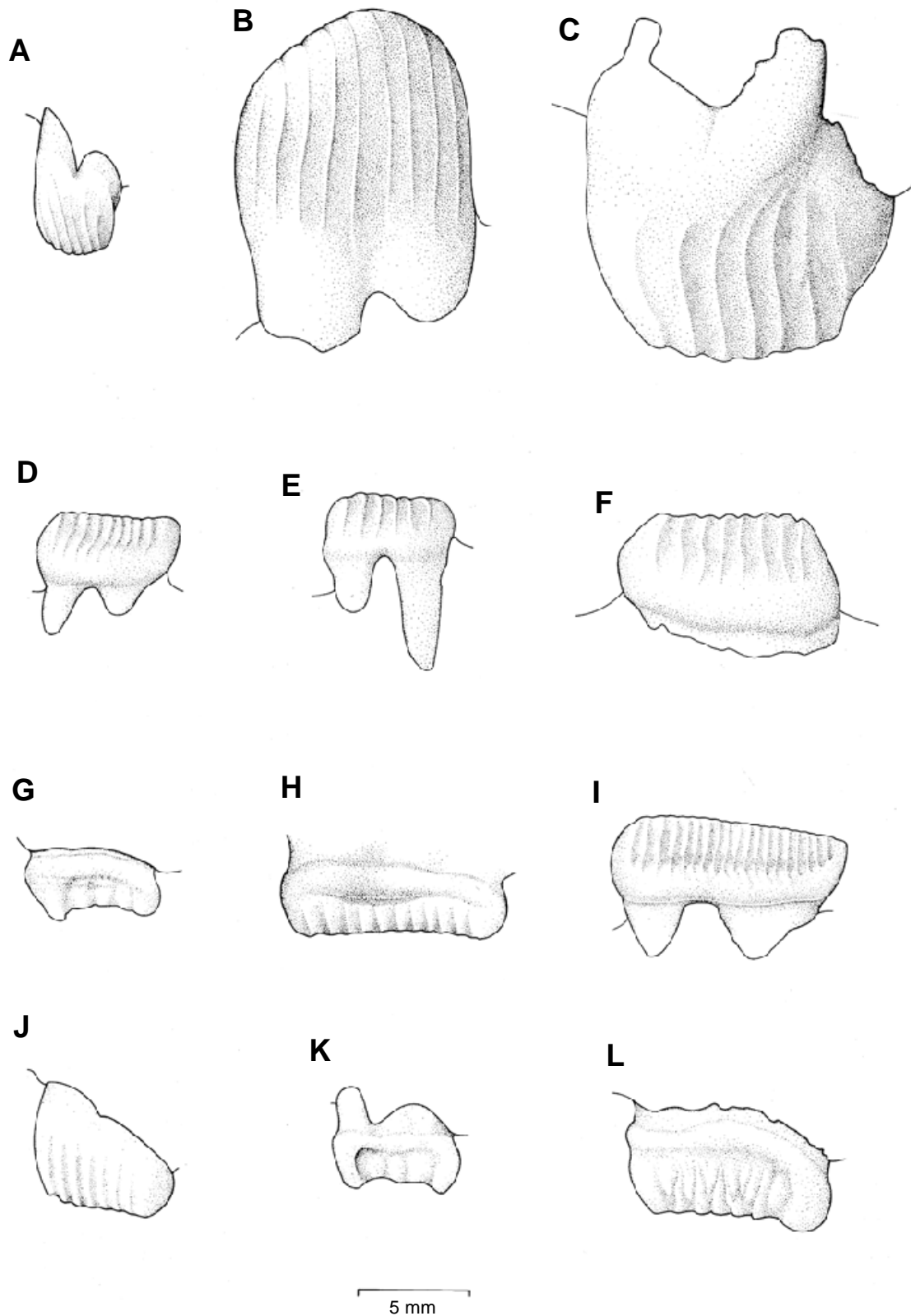


Figure 30.7 Morphology of permanent premolars (left upper or left lower PM3 except where indicated) of modern and extinct potoroid species : **A**, *Hypsiprymnodon moschatus*; **B**, *Ekaltadeta ima*; **C**, *Propleopus oscillans*; **D**, *Purtia mosaicus*; **E**, *Bulungamaya delicata*; **F**, *Wabularoo naughtoni* - right upper PM3; **G**, *Potorous tridactylus*; **H**, *Gumardee pascuali* - right lower PM3; **I**, *Wakiewakie lawsoni*; **J**, *Bettongia penicillata*; **K**, *Caloprymnus campestris*; **L**, *Aepyprymnus rufescens*. (After various sources; © ABRS) [G. Milledge]

Johnston, Davey & Seebeck (1984) concluded that the ancestral *Potorous* karyotype was similar to that of *P. longipes* ($2n=24$) and that fusion events had been important in the evolution of the Long-nosed Potoroo from this ancestral type.

The species of *Bettongia* are also similar in external appearance. Their chromosome numbers are the same (Sharman *et al.* 1980) as are their reproductive parameters (Rose 1978). The close similarity of the species may mean the animals have evolved in very similar habitats or that they have only relatively recently speciated from a common ancestor which was perhaps similar to the Tasmanian Bettong. Wakefield (1967c), in erecting a new species, the Northern Bettong (based only on museum skulls), suggested a closer relationship between the Northern and Tasmanian Bettong than between the Northern and Brush-tailed Bettong. Hayman & Martin (1974) showed chromosomal similarities between the Burrowing and Tasmanian Bettong. Sharman *et al.* (1980), after examining a specimen attributed to the Northern Bettong, stated that chromosomal criteria do not justify recognition of both the Northern and the Brush-tailed Bettong. To add to this confusion, there is some doubt as to whether Sharman *et al.* (1980) actually looked at a Northern Bettong or merely a northern Queensland specimen of the Brush-tailed Bettong (G. George personal communication). The skull of this specimen has not yet been examined.

Zuckerman (1950) showed that Tasmanian and Brush-tailed Bettongs can interbreed in captivity, but it is not known if the hybrids are fertile. All species of *Bettongia* are geographically isolated today, although not in the recent past.

Fossil Record

Fossils of members of the Family Potoroidae, as recognised here, are known from mid-Miocene (15 mybp) to Recent sediments (Archer & Bartholomai 1978; Flannery 1984a). All living species except the Northern Bettong have been found as fossils.

COLLECTION AND PRESERVATION

Collection

Modern trapping techniques usually involve the use of wire-mesh cage-traps of various designs, baited with a variety of preferred baits. Long-nosed Potoroos are easily captured in simple traps about 360 x 320 x 170 mm, with a spring-loaded door and baited with a mixture of peanut butter, honey and rolled oats. Long-footed Potoroos are taken in similar, larger traps containing the same bait, but a treadle-triggered trap has been found to be more effective. Sampson (1971) and Christensen (1980a) used large cages to capture Brush-tailed Bettongs and Rose (1985) captured Tasmanian Bettongs in similar fashion. Multiple-capture funnel-traps also have been used by Christensen (1980a) and the National Parks & Wildlife Division, Victoria to collect Brush-tailed Bettongs and Long-footed Potoroos, respectively.

Preservation

Standard museum techniques have been used for the preservation of skins, skeletal material and soft tissues of modern potoroids and for the preservation of fossil material.

CLASSIFICATION

Family Potoroidae

Subfamily Palaeopotoroinae Flannery & Rich, 1986

**Palaeopotorous priscus* Flannery & Rich, 1986

Subfamily Hypsiprymnodontinae Collett, 1887

**Hypsiprymnodon bartholomaii* Flannery & Archer, 1987

Hypsiprymnodon moschatus (Musky Rat-kangaroo) Ramsay, 1876

Subfamily Propleopinae Archer & Flannery, 1985

**Ekaltadeta ima* Archer & Flannery, 1985

**Propleopus oscillans* (De Vis, 1888)

**Propleopus wellingtonensis* Archer & Flannery, 1985

**Propleopus chillagoensis* Archer, Bartholomai & Marshall, 1978

Subfamily Bulungamyinae Flannery, Archer & Plane, 1982

**Purtia mosaicus* [*incertae sedis*] Case, 1984

*Ngama dentary

**Bulungamaya delicata* Flannery, Archer & Plane, 1982

*Kutjumarpu *Bulungamaya* species 1 [*sedis mutabilis*]

*Kutjumarpu *Bulungamaya* species 2 [*sedis mutabilis*]

*Gag site *Bulungamaya* [*sedis mutabilis*]

**Wabularoo naughtoni* Archer, 1979

Subfamily Potoroinae (Gray, 1821)

Tribe Potoroini Flannery & Archer, 1986

Potorous platyops (Broad-faced Potoroo, believed to be extinct)(Gould, 1844) [*sedis mutabilis*]

Potorous tridactylus (Long-nosed Potoroo) (Kerr, 1792)

Potorous longipes (Long-footed Potoroo) Seebeck & Johnston, 1980

Tribe Bettongini Flannery & Archer, 1986

**Gumardee pascuali* Flannery, Archer & Plane, 1982 [*incertae sedis*]

*Hamilton potoroid [*incertae sedis*]

**Wakiewakie lawsoni* [*incertae sedis*] Woodburne, 1984b

**Bettongia moyesi* Flannery & Archer, 1986

Bettongia lesueur (Burrowing Bettong) (Quoy & Gaimard, 1824)

Bettongia penicillata (Brush-tailed Bettong) Gray, 1837

Bettongia tropica (Northern Bettong) Wakefield, 1967

Bettongia gaimardi (Tasmanian Bettong) (Desmarest, 1822)

Caloprymnus campestris (Desert Rat-kangaroo, believed to be extinct) (Gould, 1843)

Aepyprymnus rufescens (Rufous Bettong) (Gray, 1837)

* Fossil forms

[After Flannery 1984a, modified by T.F. Flannery, personal communication]

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