



FAUNA *of* AUSTRALIA

32. VOMBATIDAE

R. T. WELLS



Northern Hairy-nosed Wombat—*Lasiorhinus krefftii* [D. Jew/QDEH]

DEFINITION AND GENERAL DESCRIPTION

Wombats have a suite of adaptations to their terrestrial, grazing, fossorial and nocturnal existence that clearly differentiates them from their sister group, the arboreal, browsing koalas (Phascolarctidae).

Wombats are stocky animals with short, stout, strong limbs, a short neck, a massive, broad, dorso-ventrally flattened skull and a large broad sacrum. They are plantigrade. The manus is broad and bears five forward facing digits with strong, flattened claws. The pes is narrow, slightly rotated to give a pigeon-toed stance and the hallux, or first toe (used for grasping in arboreal marsupials), is poorly developed. The tail is reduced to a vestige. The number of ribs is large: 13–15 pairs.

The rootless, continuously growing incisors and cheek teeth of wombats are unique among marsupials. The molar teeth have the form of two adjacent, dorso-ventrally arcuate, triangular columns surrounded by enamel. Cusps are present only in suckling pouch young. By the time the full dentition erupts, the occlusal surface of each cheek tooth is a flat wear face without a trace of cusps. The dental formula is $I\ 1/1\ C\ 0/0\ PM\ 3/3\ M\ 2-5/2-5$. The bullae are small and the squamosal extends into the roof of the alisphenoid hypotympanic sinus and makes a significant contribution to the anterior hypotympanic sinus.

Seven genera are recognised (two living and five extinct): *Vombatus* Geoffroy 1803; *Lasiiorhinus* Gray 1863; *Phascolonus* Owen 1872; *Phascolomys* Illiger 1811; *Rhizophascolonus* Stirton Tedford & Woodburne 1967; *Ramsayia* Tate 1951c; and *Warendja* Hope & Wilkinson 1982.

The modern genera include three living species: *Vombatus ursinus* (Shaw 1800), the forest dwelling Common Wombat of the temperate zone; *Lasiiorhinus latifrons* (Owen 1845), the Southern Hairy-nosed Wombat of the arid and semi-arid zones of South Australia; and *Lasiiorhinus krefftii* (Owen 1872), the endangered Northern Hairy-nosed Wombat of central Queensland.

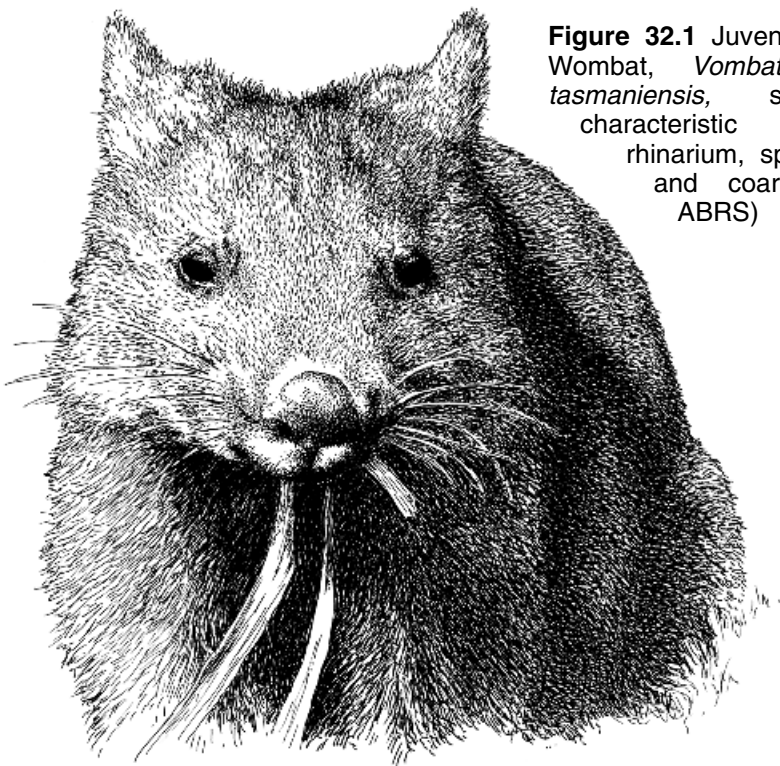


Figure 32.1 Juvenile Common Wombat, *Vombatus ursinus tasmaniensis*, showing the characteristic hairless rhinarium, split upper lip and coarse fur. (© ABRS) [K. Hollis]

Vombatus is easily distinguished by its naked leathery rhinarium, small ears and bristle-like fur. *Lasiorhinus* species have a soft furry muzzle, long ears and a silky coat.

HISTORY OF DISCOVERY

The first living wombats discovered in Australia came from Clarke Island in Bass Strait. A specimen was brought to Sydney in July 1797 aboard the *Francis* which had rescued the crew of the *Sydney Cove*, wrecked on an island in the Strait while en route to Bengal (Troughton 1941). Soon after the discovery of the Bass Strait animals, wombats were found living in the colony of New South Wales. In 1798, Governor Hunter wrote a letter to accompany the first specimen to England. He noted its similarity to a badger, that the Aborigines called it 'wombach' and that it also had been found living in New South Wales.

Wombats were found subsequently on King, Deal and Flinders Islands in Bass Strait and given the name *Didelphis ursina* Shaw 1800. The subsequent discovery and naming of various fossils and subspecies by different authors greatly confused wombat taxonomy.

The name *Opossum hirsutum* Perry 1810 probably applied to the mainland form (Troughton 1941). In 1838, Owen described a fossil wombat, collected by Sir Thomas Mitchell in his exploration of the Wellington Caves in New South Wales, as *Phascolomys mitchelli*. Owen was unaware of the living mainland form, but the island form he knew as *Phascolomys vombatus* Leach 1815. In 1845, Owen received a skull of the Southern Hairy-nosed Wombat from Mt Gambier in South Australia, which he named *Phascolomys latifrons* Owen 1845. He was later to examine the skulls of the living mainland Common Wombat which he saw as distinct from the Wellington species and gave it a new name, *Phascolomys platyrhinus* Owen 1853. Although Owen clearly differentiated the 'platyrhine' wombats (*Vombatus* species) from the 'latifrons' species (*Lasiorhinus* species), he referred them to the same genus, *Phascolomys* Illiger 1811. Murie (1865) placed Owen's 'latifrons' species in the genus *Lasiorhinus* Gray 1863.

The taxonomy of the Vombatidae was further complicated by the description of a large number of small fossil forms, the inclusion of the Tasmanian Common Wombat as a subspecies and the recognition of a number of subspecies of the Southern Hairy-nosed Wombat. The small fossil forms include *Phascolomys krefftii* Owen 1872, from Wellington Caves, New South Wales; *Phascolomys thomsoni* Owen 1872, *Phascolomys parvus* Owen 1872; *Phascolomys angustidens* De Vis 1891, from the eastern Darling Downs, Queensland; *Phascolomys pliocen* McCoy 1866, from Dunolly, Victoria; *Phascolomys hacketii* Glauert 1910, from Mammoth Cave, Western Australia and *Warendja wakefieldi* Hope & Wilkinson 1982, from McEacherns Cave in southwestern Victoria.

Dawson (1983a) examined the variation in character states in the Vombatidae and supported Tate's (1951c) division of the Common Wombat, *Vombatus ursinus*, into four subspecies: *V. u. ursinus* (Shaw 1880) from Flinders Island; *V. u. tasmaniensis* (Spencer & Kershaw 1910) from Tasmania; *V. u. platyrhinus* (Owen 1853) from eastern mainland Australia, and; *V. u. mitchelli* (Owen 1838), a fossil population from Wellington Caves, New South Wales. *Phascolomys pliocen* McCoy 1866, *Phascolomys parvus* Owen 1872 and *Phascolomys thomsoni* Owen 1872 were assigned by Dawson (1983a) to *Vombatus ursinus* (Shaw 1880), while *Phascolomys hacketii* Glauert 1910 is retained as a distinct species, *Vombatus hacketii*. In Dawson's revision, all the Northern Hairy-nosed Wombats become *Lasiorhinus krefftii*. They include *Phascolomys gillespiei* De Vis 1900 from the Moonie River in southern Queensland, *Lasiorhinus latifrons barnardi* Longman 1939 from Clermont in central Queensland and

Phascolomys krefftii Owen 1872 from Wellington Caves, New South Wales. *Phascolomys angustidens* De Vis 1891 is tentatively assigned to the genus *Lasiorhinus* (Dawson 1983b).

Crowcroft (1967) examined interpopulational variation in *Lasiorhinus latifrons* and concluded that the differences are insufficient to warrant division into subspecies.

Three large fossil wombats were described by Owen (1872): *Phascolomys medius*, *Phascolomys magnus* and *Phascolonus gigas*, with *Phascolonus* proposed tentatively as a subgenus. Owen also described some large blade-like incisors of an animal he named *Sceparnodon*. Lydekker (1891) associated *Sceparnodon* with the missing incisors of *Phascolonus*, an association which was later confirmed by Stirling & Zietz (1899), when they discovered a more complete skull at Lake Callabonna in South Australia. Recently, Dawson (1981) synonymised *Phascolomys curvirostris* Owen 1875 and *P. magnus* Owen 1872 in *Ramsayia magna* (Owen 1872). Dawson further suggested that *Phascolomys lemleyi* Archer & Wade 1976 also should be placed in *Ramsayia*.

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The Common Wombat has bare, granular skin between the nostrils and coarse, brown buff, bristle-like fur with no special markings. It has small rounded ears that are well furred on the outer surface. In contrast, *Lasiorhinus* species have a soft pig-like muzzle and the region between the nostrils is covered with pale, often white, velvety fur. Their pelt colour varies from light to dark grey, being darkest above the forequarters. Different colour morphs are known, with the most common variant being yellow-brown (Angas 1861; Krefft 1872). The ears are narrow, pointed and sparsely furred on their outer surface (Figs 32.1 & 2).

Wombats are strong, stocky animals with short fore- and hind legs of approximately equal length. Wombats walk on the soles of their feet. The forefeet have five forward facing digits with strong flattened claws. The hind feet are narrow and slightly rotated to give a pigeon-toed stance. The first toe is reduced to a small nubbin lacking a claw and the syndactylous second and third toes are conjoined in a sheath of skin, with only their terminal joints free and

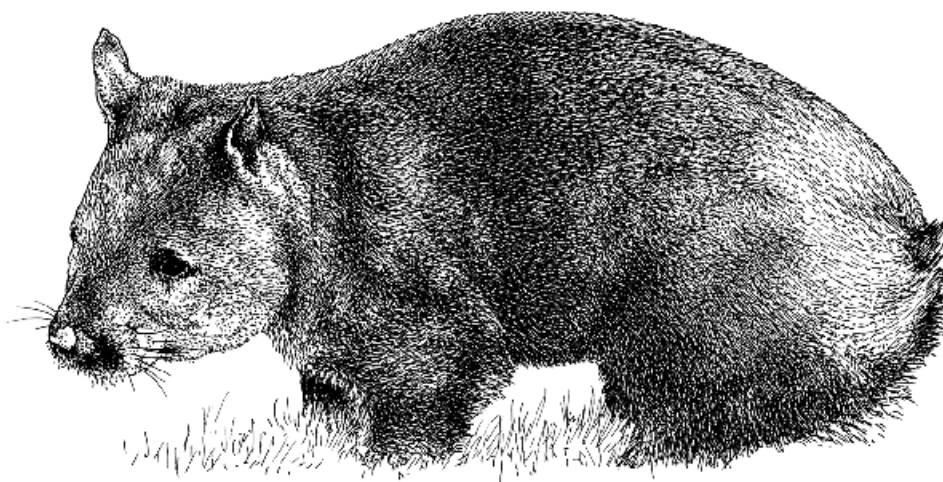
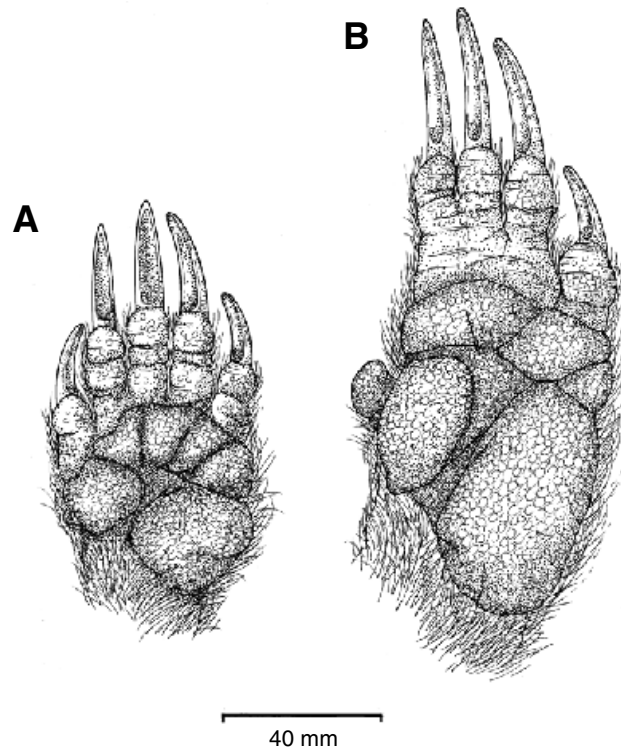


Figure 32.2 Adult *Lasiorhinus latifrons*, showing species characteristics: long ears, fine coat and soft hairy muzzle. (© ABRIS) [K. Hollis]

bearing long, strong claws. The fourth toe is slightly shorter and the fifth much shorter than the third and both have well-developed claws (Fig. 32.3). The short vestigial tail is hidden by body fur.

Figure 32.3 Common Wombat, *Vombatus ursinus*. **A**, left manus; **B**, left pes, showing the long, flattened claws adapted for digging. The clawless first digit (hallux) of the pes is reduced to a small nubbin, Digits II and III are syndactylous. (After Jones 1924; © ABRIS) [T. Cochran]



The skull is massive, broad and flattened. Merrilees (1967) reassessed the characters used by Owen to distinguish different taxa. He found that characters of the incisors, premolar teeth, palate, cranial bones and mandible were sufficient to separate the modern species at the generic level (Fig. 32.4).

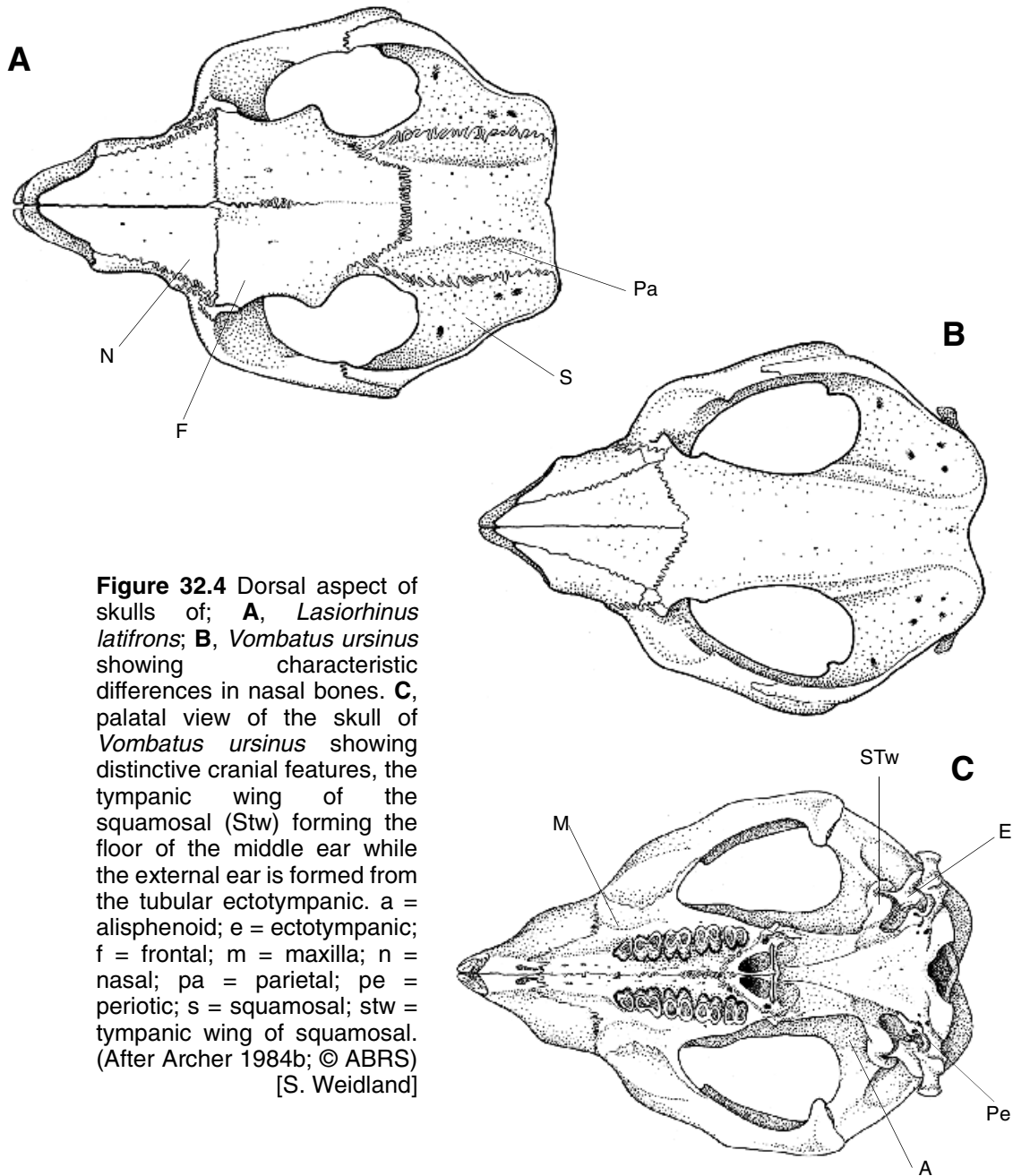
The lower incisors are low, wide, and are almost spatulate in wombats. Those of Hairy-nosed Wombats are high and narrow. The palate is narrow between the first molars of Common Wombats, but wide in Hairy-nosed Wombats. The remaining nineteen cranial and mandibular characters used by Merrilees (1967) show some degree of overlap, but in combination can be used to separate the two genera.

All wombats have continuously growing incisors, premolars and molars. As an animal grows older, the teeth increase in length and width, leading to an increase in the overall length of the tooth row (Merrilees 1967) (Fig 32.5).

The Common Wombat weighs about 23 kg, with a maximum of 38 kg, has a head and body length of 850 mm, (maximum 1140 mm) and a tail length of 25 mm (Green 1973; McIlroy 1976). Island forms are generally smaller. The Southern Hairy-nosed and Northern Hairy-nosed Wombats weigh 19–32 kg, and have a head and body length of 772–934 mm and a tail length of 25–60 mm (Crowcroft 1967).

Body Wall

Hair and sensory vibrissae appear early in pouch life (Jones 1924; Boardman 1943). Hair tracts radiate caudally and ventrally on the head and trunk in two streams commencing at the nose. Hair radiates postaxially on the limbs. This simple pattern is in marked contrast to the complex hair tracts of the Koala.



Vibrissae are grouped into: seven genals; twelve interramals (three long and three short each side); mysticals long and coarse, in poorly defined rows, reaching well beyond the eye; submentals (short and curving forwards). Brachial vibrissae also are present at the carpus (Jones 1924).

The size and shape of homologous foot pads vary within and between species (Jones 1924; Boardman 1943).

The Common Wombat shares a number of myological features with the phalangerids and pseudocheirines (Sonntag 1922). These include inseparability of the prevertebral muscles, an undivided rhomboideus, fusion of the trapezius with the pectoral fascia and clavicular deltoid and a single head to the biceps flexor cursis. The Common Wombat differs from the phalangerids and phascolarctids in the absence of a quadratus femoris, an obturator internus and popliteus and it has only a single head to the rectus femoris.

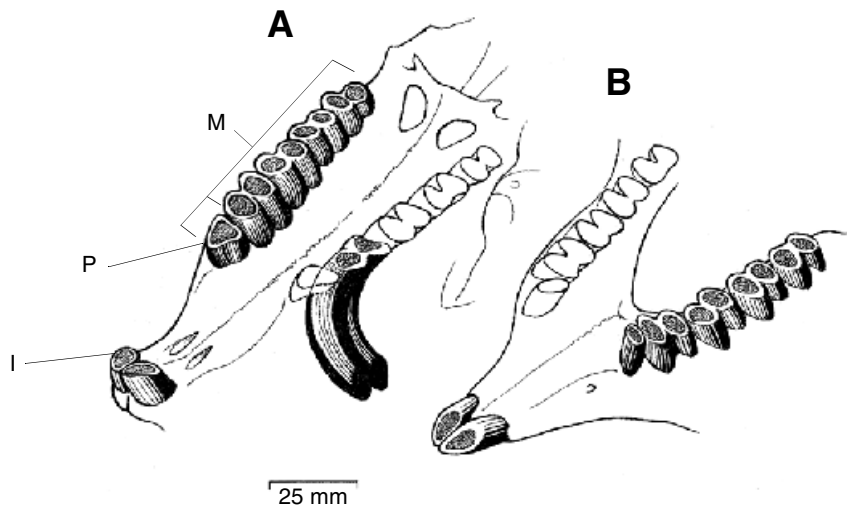


Figure 32.5 Upper **A**, and lower **B**, dentition of *Vombatus ursinus*, with an 'x-ray' view of PM² illustrating the curvature and open roots of the continuously growing teeth. Hatched areas indicate where the original enamel caps have been worn away to expose the softer dentine. I = incisor; P = premolar; M = molar. (After Archer 1984b; © ABRS) [F. Knight]

Skeletal System

The wombat skeleton (Fig. 32.6) is characterised by a large, broad, dorso-ventrally flattened skull and a relatively short neck. The strong pectoral girdle is associated with short powerful forelimbs. The humerus is short and broad, the radius and ulna robust. The thorax is long and broad with a relatively large number of ribs (Hairy-nosed Wombats 13 pairs, Common Wombat 15 pairs). The pelvis is strong and broad with a marked outward flaring of the ilial blades. The hind limbs are slightly longer than the forelimbs, yet equally robust. The fibula is well developed. The manus and pes are plantigrade and bear long flat claws. The epipubic bones are long and broad and the tail is short.

Hairy-nosed Wombats have seven cervical, 15 thoracic, four lumbar, four sacral, and 15–18 caudal vertebrae; The vertebral formula in Common Wombats deviates from the above in the presence of 10–12 caudal vertebrae. The pronounced olecranon process of the ulna, the prominent deltoid crest of the humerus, the strong scapular spine and acromion process and the robust clavicle are indicative of a strong forelimb musculature, ideally adapted for burrowing. The skeleton of the extinct *Phascolonus gigas* is similar to, but approximately twice the height and girth of *Vombatus*. Whether it also burrowed is a matter of speculation. Owen (1877) provided a detailed description of the skeleton of *Vombatus* and Stirling (1913) of *Phascolonus*.

Locomotion

No detailed analyses of wombat locomotion have been carried out. Field observations and cinematographic analysis (Wells 1978a) of the Southern Hairy-nosed Wombat indicate three gaits: walk, trot and bound. The transition speeds between gaits are not known, but one individual was paced at 40 km/h over a distance of approximately 150 m (Wells 1984). They cannot sustain a bounding gait and soon tire.

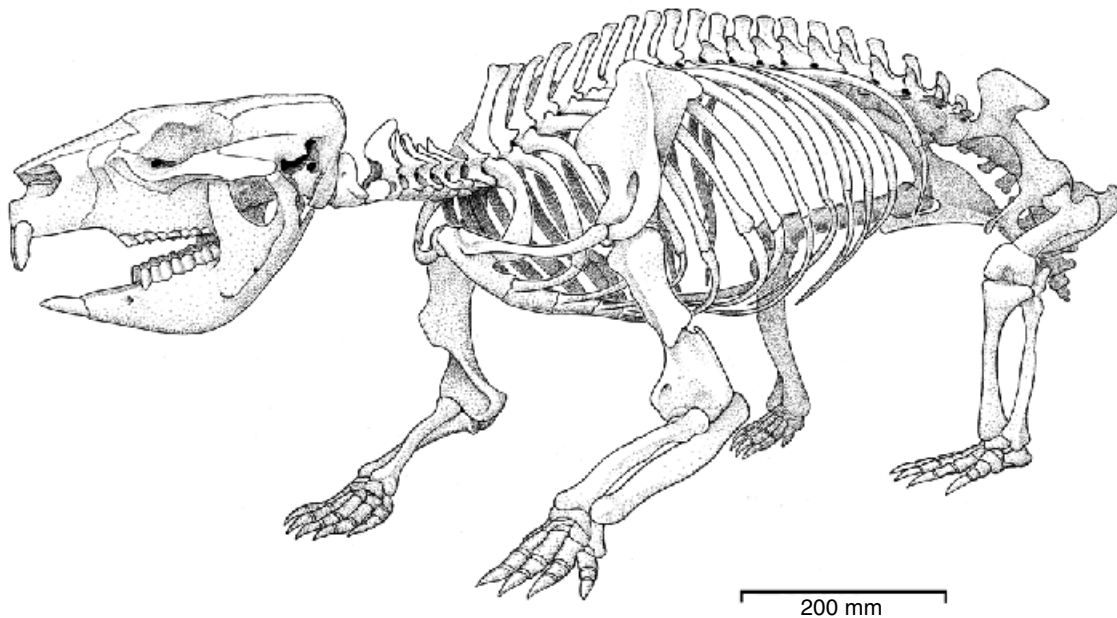


Figure 32.6 The skeleton of *Lasiorchinus latifrons* showing the flattened skull, powerful forelimbs, short neck, broad pelvis and short tail, all adaptations to a fossorial life. (© ABRS) [G. Milledge]

Wombats use the forepaws for excavation and the incisor teeth to remove obstacles. To excavate the sides and roof of a tunnel they twist the forward portion of the body, rolling almost onto their backs. Spoil from the excavation is pushed back by the hind limbs. A wombat may reverse all the way out of its burrow, kicking the spoil behind it. The dimensions of a burrow are such that an animal may obstruct it completely with the broad sacral area of the back. Notwithstanding, wombats can turn around in a burrow by performing a barrel roll aided by the short and powerful forelimbs.

Feeding and Digestive System

Wombats are grazing mammals (Wells 1968, 1973, 1978a; McIlroy 1973; Mallett & Cooke 1986). Grasses and forbs constitute their principal food. The suggestion has often been made that they are rhizophagous (root eaters). Stirling (1913) noted that in the drier parts of their range they habitually eat the leaves and stems of various kinds of low growing shrubs, particularly Bluebush (*Maireana* species). He also noted that, like pigs, they will root up 'various grasses, tuberous or bulbous rooted plants, some of which are known locally as 'yams', the rhizomes of ferns and many others'. Stirling (1913) reported that the consensus amongst naturalists is that wombats will only dig up the roots of larger trees when green grass and surface water is not available and that they particularly favour the roots of the 'smaller Eucalypts', possibly to obtain the watery sap, as did Aborigines and bushmen. Wakefield (1961, 1967b) reported that Common Wombats habitually chew the bark of Stringybark (*Eucalyptus baxteri*) and the roots of Apple Box (*E. bridgesiana*) to obtain the sap.

The preferred diet, however, would appear to be green grasses, particularly fresh shoots. Kershaw (1909) described Common Wombats pulling clumps of grass apart to reach the greenest stems. Grazing by wombats within proximity of the warren tends to produce a 'lawn' of green shoots, delaying the onset of maturation of individual grass plants (Wells 1978a).

The ability of wombats to select their food is aided by their split upper lip. This allows them to place the incisors very close to the ground and pluck the tiniest green shoots. Olfactory senses presumably play an important role in food selection for these nocturnal animals.

Once ingested, food is macerated thoroughly. In a comparative study, Wells (1973) found the mean particle size in Southern Hairy-nosed Wombat faeces to be half that of the Western Grey Kangaroo, *Macropus fuliginosus*, grazing on the same pasture. Dierenfeld (1984) compared faecal and stomach content particle sizes from rabbits, hairy-nosed wombats and red and grey kangaroos. Wombats had the smallest mean particle size (342 μ) of stomach contents, even though the wombat diet contained more fibre than that of the rabbit. This ability to finely triturate their food correlates with continuously growing teeth and a simple alimentary canal.

The teeth of wombats, like those of all grazing mammals, are subject to considerable wear from silica inclusions (phytoliths) in plant cells. In droughts, wombats tend to ingest considerable amounts of soil in the process of feeding (Dierenfeld 1984), also adding to tooth wear. The open-rooted, continuously growing teeth, with their core of soft dentine and margin of hard enamel, ensure the maintenance of an efficient dental mill.

The wombat gut is remarkably simple for a grazing herbivore. There is neither a forestomach nor a well-developed caecum for fermentation of cellulose. The digestive tract is approximately 10–11 times the wombat's head and body length (Gowland 1973; Dierenfeld 1984). The tract is approximately eight times longer than that of the Red Kangaroo, *Macropus rufus* and the Western Grey Kangaroo (Dierenfeld 1984), but very much shorter than in ruminant herbivores, where it is greater than 20 times the head & body length (Dukes 1955).

Descriptions of the alimentary canal of wombats range from general accounts of the intestines and location of the caecum (Owen 1836, 1868; Lönnberg 1902; Mitchell 1916; Hill & Rewell 1954; Arvy 1973) to detailed descriptions of the gastrointestinal tract (Mackenzie 1918b). There is a dearth of detailed anatomical studies of the wombat gut, with some workers, such as Knox (1826), even confusing koalas for wombats in their examinations.

In gross morphology, the wombat stomach is simple and not very large — about 9% by weight of the alimentary canal and digesta in the Common Wombat (Gowland 1973) and the Southern Hairy-nosed Wombat (Dierenfeld 1983). An area of highly specialised secretory cells is found on the lesser curvature of the stomach, the cardiogastric gland (Hingson & Milton 1968; Milton, Hingson & George 1968). Secretions from the stomach mucosa and cardiogastric gland are the most probable source of the low pH stomach contents of pH 2.5–4 in the Southern Hairy-nosed Wombat (Wells 1968), and pH 4 in the Common Wombat, (Gowland 1973).

The caecum is small and not unlike the vermiform appendix in man, while the colon is quite large, with a sacculated proximal end. These sacculations decrease in size with distance from the ileocaecal valve. The proximal colon is divided from the distal colon in the Common Wombat by a pair of "outpouchings" from the main canal. These have been referred to as a second caecum by early anatomists. The pouches are fixed by mesentery to the abdominal wall near the stomach (Gowland 1973). Lying in close proximity to the fixed pouches, the stomach and the duodenal loop are a simple mass of pancreatic tissue. The pH range of the contents of the small intestine and colon is 6.5–7.5.

Small rugosities cover the internal surface of the small intestine and proximal colon. The internal surface of the pouches and distal colon is smooth. There is no distinct boundary between the distal colon and rectum. The colon in wombats is large: in the Common Wombat and the Southern Hairy-nosed Wombat it represents 54% and 64% total gut length, respectively; 73% and 78% total gut weight; and in the Common Wombat, 68% gut volume (Gowland 1973; Dierenfeld 1984). Throughout the caecum, colon and rectum, glands of Lieberkühn are very common. They also occur in the small intestine, but are in much smaller numbers and lie between villi.

The small stomach, with gastric glands and low pH, is an unsuitable environment for microbial digestion and suggests that the wombat is a post-gastric fermenter. Yet, unlike other post-gastric fermenters, the caecum is quite small. The sacculated hindgut, with its neutral pH, approximately 12.5% water content (Gowland 1973; Dierenfeld 1984) and large numbers of mucous-secreting glands, would appear to be the functional analogue of the kangaroo fore-stomach and the major site of bacterial fermentation.

Wells (1968, 1973) could not find evidence of coprophagy in wombats, suggesting that they gain sufficient protein from the cytoplasm of plant cells and/or that their dietary protein requirements are quite low. This may be the case in Hairy-nosed Wombats, which have a generally low resting metabolic rate (Wells 1978b). The situation in the Common Wombat is unclear. The resting metabolism in this genus appears to be closer to that predicted (Dawson & Hulbert 1970) for a marsupial of similar body weight, hence a greater protein turnover might be expected. Foster, Hume & Barboza (1986) reported a maintenance nitrogen requirement of 212 mg/kg body weight $d^{-0.75}$ for Common Wombats, similar to the value of 205 mg/kg body weight $d^{-0.75}$ for Southern Hairy-nosed Wombats reported by Wells (1973). Regardless of the protein question, the fermentative breakdown of cellulose in the colon may be an important supplementary source of energy to the wombat.

Clearly, the whole question of digestion and metabolism in wombats is worthy of further investigation.

Circulatory System

There are few studies of the circulatory system. Wade (1968) discussed structural characteristics of the heart of Southern Hairy-nosed Wombat and Lee & O'Shea (1977) the vasculature of the reproductive tract of the Common Wombat. The arteries and veins of both the male and female reproductive organs are in apposition, suggesting the existence of a counter current system. The functional significance of this has not been investigated.

Respiration

Withers (1972) investigated respiratory adaptations in Southern Hairy-nosed Wombats to the hypercapnic and hypoxic conditions expected within a burrow. The response to inspired carbon dioxide was variable: respiratory rate, depth and 'minute' volume generally increased, yet sometimes decreased, even at 10% CO₂. This hypercapnic response differed both between individuals and the same individual on different days. The rather labile response to CO₂ and consequent tolerance of acidosis is of obvious advantage to a burrowing mammal (Darden 1972). Of the possible adaptations to decreased oxygen tensions, Southern Hairy-nosed Wombats exhibited a small respiratory reserve, some flow reserve (tachycardia), no erythropoietic reserve and some chemical reserve (Bohr effect present, but no 2,3 D.P.G. effect).

Excretion

The only studies of water requirements and excretion are those of French (1965) and Wells (1973) for the Southern Hairy-nosed Wombat. The wombat kidney is simple in structure and does not have the elongate papilla typical of desert mammals. Maximum urine concentrations of 3100 mosmol are obtained after 21 days of dehydration, with a concomitant drop in faecal moisture to 38%. The latter is at the limit for water extraction from a faecal pellet by mechanical means (French 1965). Wombat faeces are amongst the driest recorded for a mammal.

Rates of water turnover of Southern Hairy-nosed Wombats measured under field and laboratory conditions are exceedingly low: values of 22 ml/kg body weight per day are not uncommon for field animals (Wells 1973). The key to water conservation in the species lies in their behaviour. They avoid extremes of high ambient temperature and low humidity by living in a burrow and breathing air close to saturation for the burrow air temperature (18–21°C throughout the year). They emerge to feed at night when conditions of temperature and humidity outside the burrow approach those inside.

In summer, their activity shifts to early morning and in winter to early evening (Wells 1978b). The summer shift also increases the probability of gaining hygroscopic water and dew from plants. Such shifts in activity lead to a considerable saving in respiratory water loss of 57%. In water-deprived laboratory animals, respiratory and cutaneous water loss together account for 77% of total loss, urine accounts for 17% and faeces for 5%. In the field, changes in total body water parallel changes in faecal water while plasma electrolyte (Na^+/K^+) levels show little change. Wells (1973) suggested this may reflect water loss from the gut. Within 12 hours following rehydration in water deprivation trials, wombats regained half the total body weight lost over 21 days without any apparent change in plasma electrolyte levels (Wells 1973).

There is some evidence that Southern Hairy-nosed Wombats can recycle urea as Wells (1968) reported a ten fold difference in urinary urea/plasma ratios for animals on high and low nitrogen diets. Whether this recycled urea is utilised by gut bacteria is not known.

Sense Organs and Nervous System

The large gyrencephalic brain of wombats differs from other diprotodontans in its ovoid form and reduced parafloccular lobes, characters shared with the extinct thylacoleonids (marsupial lions) (Haight & Murray 1981; Archer 1984b). Johnson, Haight & Megirlan (1973) noted that in *Vombatus* the relationship between the convolutions of the neocortex and mechanosensory function is similar to that observed in placental carnivores.

The lateral position of the eyes of wombats results in a large lateral monocular field and a small frontal binocular field. The retina of the Southern Hairy-nosed Wombat has a well-developed visual streak yet lacks an area centralis (Tancred 1981), features of an animal sensitive to movement along a horizontal field of view. This is reflected in the retinal wiring of the Southern Hairy-nosed Wombat, in which the monocular segment of the lateral geniculate nucleus is about twice that of the binocular segment (Sanderson & Pearson 1981). The accessory optic system of the Southern Hairy-nosed Wombat is unusual among marsupials in that it receives a bilateral projection from the retina and there is considerable overlap of the retinal fibres from the two eyes in the superior colliculus (Sanderson & Pearson 1981). The level of complexity in the optic

system of the Southern Hairy-nosed Wombat approaches that of primates and carnivores. The nature of the visual information received by the lateral geniculate nucleus warrants further study.

Endocrine and Exocrine Systems

In the absence of histological studies, there is some indirect evidence that wombats lack functional sweat glands. This is not unexpected in a burrowing animal that, by behaviour, avoids high ambient temperatures. When heat stressed, wombats roll on their back and expose the sparsely furred axillary regions (Wells 1973, 1978b; Strezlecki 1974). Common Wombats may also salivate.

Reproduction

The gross anatomy of the reproductive system has been described by MacKenzie & Owen (1919a) and Pearson (1944) for the Common Wombat and by Brooks, Gaughwin & Mann (1978) and Gaughwin (1981) for the Southern Hairy-nosed Wombat.

The testes are located in a prepenile scrotum. The scrotum is never pendulous nor is there a well-developed pampiniform plexus or pigmented tunica vaginalis, features normally associated with the control of testicular temperature in hot environments. Testicular size varies with season and maturity. The cauda epididymis is tightly encased within a sheath formed by the tunica vaginalis. Brooks *et al.* (1978) suggested that temperature regulation of sperm, below that of the rest of the body, may occur here rather than in the testis. Sperm of both groups of wombats are morphologically similar and resemble those of the Koala (Hughes 1965; Brooks *et al.* 1978).

The prostate is of a carrot-like shape, common to marsupials, and consists of three distinct segments. Each of the three pairs of Cowper's glands is surrounded by striated muscle. Glands A and B (Brooks *et al.* 1978) are histologically distinct from Gland C. Secretions of the prostate and Cowper's glands A and C have been investigated in The Southern Hairy-nosed Wombat. Brooks *et al.* (1978) suggested that interactions between the glandular secretions after ejaculation are related to the formation of a copulatory plug left in the vaginal sinus.

The penis is approximately 100 mm long. The glans penis is bifurcate for approximately 15 mm from the distal end and posterior to this is a series of backward facing spines. The retracted penis is held in an S-bend by the retractor muscles.

Several histological studies of the ovaries have been carried out: O'Donoghue (1916) for the Common Wombat and Fraenkel (1905) and Gaughwin (1981) for the Southern Hairy-nosed Wombat. Both groups of wombats are essentially similar, anatomically and histologically. In this respect, they are characterised by the presence of much interstitial tissue. Anatomically, they are ovoid, but rather flattened on the dorsal aspect. Corpora lutea are yellowish and highly vascularised. Translucent Graafian follicles are easily seen on the surface of the ovaries of lactating and pregnant females and may be up to 10 mm in diameter (Gaughwin 1981).

The uteri in anoestrus adult and juvenile wombats are similar in size to the fallopian tubules; in pregnant animals they are greatly enlarged, decreasing in size in lactating animals. The uteri open into the median vagina or vaginal cul-de-sac. A well-defined septum, extending for half the length of the median vagina, separates the opening of the uteri and lateral vaginae of each side. In juvenile animals, the median vagina does not connect with the urogenital sinus. In adults, it connects to the urogenital sinus just above the opening of the

bladder. In the Southern Hairy-nosed Wombat, there are two pairs of urogenital sinus glands (Gaughwin 1981). Their function is unknown, but they increase in size during pregnancy.

The pouch condition varies with reproductive status. In anoestrous and juvenile animals, the two teats are small, the pouch shallow, clean, dry and the sphincter muscles poorly developed. In oestrous females, the pouch becomes moist, increases in depth, one teat elongates and the sphincter muscles are well developed.

Embryology and Development

Other than some preliminary growth data on pouch young and development of hair tracts, little is known of the embryology and development of wombats.

NATURAL HISTORY

Life History

Wombats are seasonal breeders. The timing of reproduction, however, appears to vary both within and between species. Mallett & Cooke (1986) reviewed the data for the Common Wombat. In this species, timing of reproduction correlates with both latitude and altitude, such that weaning of young coincides with the maximum potential growth period of temperate grasses, usually during summer months. The reproductive cycle in the Southern Hairy-nosed Wombat also correlates with the germination and growth of native pasture (Wells, Boreland & Forward 1986). In this case, weaning occurs in spring or early summer, almost 6 months out of phase with the Common Wombat, and is tied to the winter rainfall patterns of the arid and semi-arid zones of South Australia.

In both groups gestation is short, approximately 21 days. Young first leave the pouch at approximately 8 months, vacating it permanently at 9 months. They are fully weaned at 12 months. During this time they grow very rapidly. Wombats may double their body weight within 3–8 months of weaning. Under ideal conditions they approach adult body weight in just over 2 years, but under field conditions adult size and reproductive maturity are usually not attained until 3 years. Dispersal of young may occur any time after 2 years. Dispersing young often show evidence of attack by other wombats, such as bites to the pelt and ears. They either establish themselves in vacant warrens or burrows or establish new burrows at the edge of the population range (McIlroy 1973; Wells 1973).

The age of pouch young and juvenile wombats may be estimated from measurements of body length (Boardman 1943; Conder 1970; Wells 1978; Presidente 1982b). In an animal with continuously growing teeth, there is no non-invasive means of estimating the age of adults. Life table data can be compiled only by monitoring the lives of marked individuals.

Wombats, captured as adults, have been kept in captivity for more than 17 years (Flower 1931; Crandall 1973). Adult Southern Hairy-nosed Wombats tagged in the field in 1968 survived until the drought of 1982–83 (R.T. Wells, personal observation). Survival and recruitment of Southern Hairy-nosed Wombats would seem to be mediated primarily by rainfall distribution and its concomitant effect on pasture growth (Wells 1973, 1978a) rather than by predators.

Vulnerable periods for this species include pouch life, where survival is dependent on the mother's milk supply which may cease in drought years; at weaning, in late winter or early spring, when young require high quality green pick; and at recruitment into the adult population when individuals, particularly

young males, attempt to establish or integrate with other individuals in a warren. Continued harassment within the warren social structure in a poor year may lead to a drop in condition, possibly death (Wells 1978a).

The Southern Hairy-nosed Wombat requires a minimum of 2, and generally 3 years of effective rainfall consecutively for recruitment of young. Further, there must be April rains to promote germination and growth of pasture before the onset of winter. Green pick will then be available at weaning in early spring. The percentage of years in which effective rains occurred in April over the range of the Southern Hairy-nosed Wombat is shown in Figure 32.7. The drought frequency over the same range is shown in Figure 32.8 (after Trumble 1948). These data suggest that recruitment for this species may be episodic.

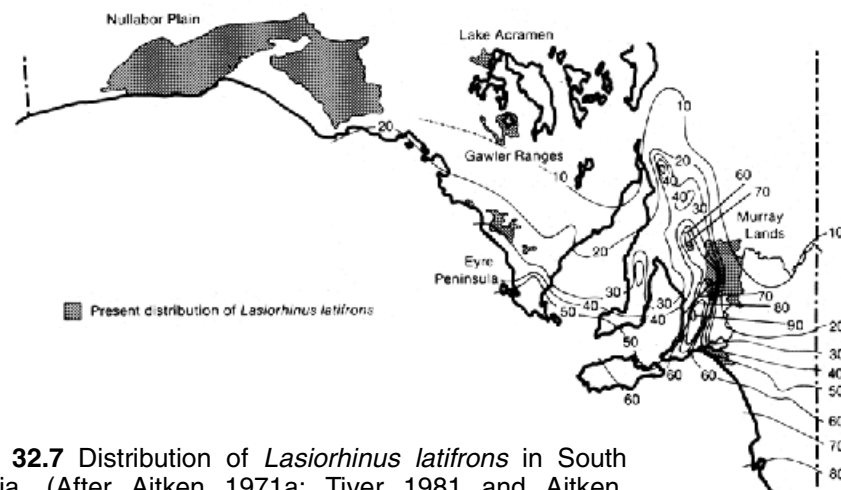


Figure 32.7 Distribution of *Lasiorhinus latifrons* in South Australia. (After Aitken 1971a; Tiver 1981 and Aitken, unpublished data) along with the percentage of seasons with effective April rainfall. (After Trumble 1948). Much of the current range of the wombat lies within the 10 to 20% isoclines. Thus over approximately the last hundred years of rainfall records there have been less than 20 years in which rainfall distribution would favour survival of juvenile wombats.

There are insufficient long-term data on this species to construct a life table. An ongoing mark–release–recapture program by the South Australian National Parks and Wildlife Service, however, has this as a long term goal.

There is little information on sex and age class survival of *Vombatus*. There is some evidence to suggest that predation by dingoes may play a role in regulating numbers (Newsome, Catling & Corbett 1983b; Triggs, Brunner & Cullen 1984). Nicholson (1963) reported that young dig small burrows within the maternal burrow as protection from predators. McIlroy (1973) suggested that road kills and predation by man and dingoes were the major sources of mortality in the Central Highlands. Mallet & Cooke (1986) suggested that land clearing and changes in pasture composition due to grazing by rabbits and domestic stock may be limiting populations at the western edge of their range.

Ecology

As both groups of wombats are grazers, the availability of pasture is an important habitat requirement. In the case of the Common Wombat, high sloping ground is favoured for burrow drainage and some form of forest cover is important for predator avoidance (McIlroy 1973; Mallet & Cooke 1986). Hairy-nosed Wombats occur in more arid regions with a wide range of vegetation types (Aitken 1971a; Crossman & Gordon 1986). Although a well-developed soil

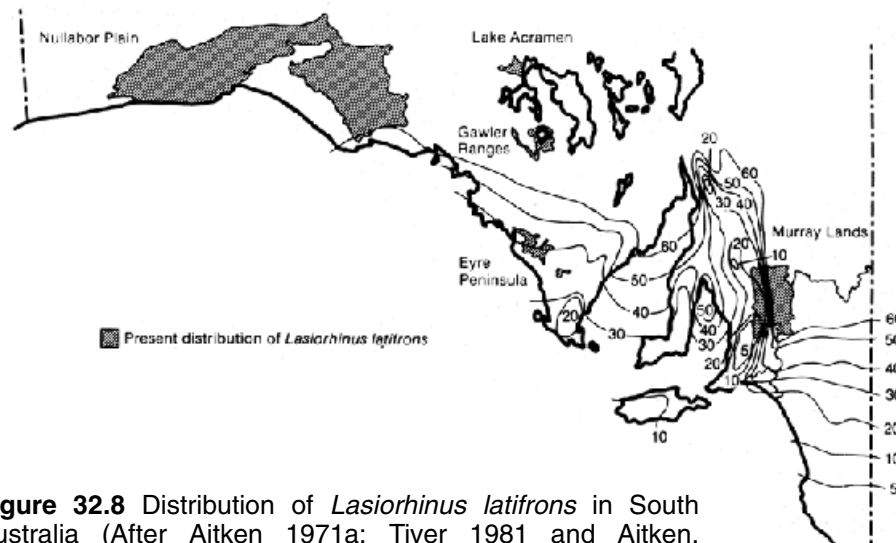


Figure 32.8 Distribution of *Lasiorchinus latifrons* in South Australia (After Aitken 1971a; Tiver 1981 and Aitken, unpublished) along with the frequency of drought. (After Trumble 1948). Over much of their range wombats experience >60% drought frequency.

carbonate (calcrete) occurs over much of their range, it does not seem to be essential for burrow stability since warrens also occur in sandy country (Aitken 1971a; Crossman & Gordon 1986).

Recent work (Mallet & Cooke 1986; Wells *et al.* 1986) focused attention on the importance of pasture composition in the recruitment of young. Over-grazing by rabbits and domestic stock has altered pasture species mixes from perennials to annuals and has shifted the period of maximum productivity out of phase with wombat breeding cycles. Aitken (1971a) noted the correlation between the spread of rabbits and decline in populations of the Southern Hairy-nosed Wombat, with subsequent recovery following the spread of myxomatosis. Mallet & Cooke (1986) also noted this correlation with the decline of the Common Wombat in South Australia. The hypothesis that rabbits are of major importance in the decline of wombat populations requires further testing.

Although wombats harbour large numbers of ecto- and endoparasites (Doube 1981), these appear to have minimal effect on general health (Gaughwin 1982). Bacterial, fungal and protozoal induced diseases occur in wild wombats (Doube 1981), but rarely appear to be debilitating.

Behaviour

The focus of the Southern Hairy-nosed Wombat social organisation is the warren. A large warren may have 10 or more burrows, many of which are interconnected. One warren may be inhabited by up to 10 wombats, although all individuals may not be present at all times (Wells 1973, 1978a; Gaughwin 1981). Some burrows may be preferred by individuals although there is no evidence of burrow ownership among warren occupants. Females show greater burrow preference than males. There are well-defined dominance relationships among males in a warren while females appear to be subordinate to all adult males (Gaughwin 1981).

In contrast, the burrow is the focus of Common Wombat activity. An individual may use up to 11 burrows over its range, although most activity is confined to three or four burrows. Home ranges of individuals often overlap and multiple burrow use is common. Semi-exclusive feeding areas occur within overlapping home ranges, suggesting some form of territoriality (McIlroy 1973).

Territoriality is the major interwarren relationship between Southern Hairy-nosed Wombat males. Territoriality in both *Vombatus* and *Lasiiorhinus* is probably maintained by olfactory cues and, occasionally, by fighting and chasing. Warrens (Southern Hairy-nosed Wombat) and burrows (Common Wombat) are connected by a network of trails. Rubbing posts are common around the warren or the semi-exclusive feeding area. Wombats have anal scent glands, a common feature in nocturnal species. The rubbing of posts, logs and overhanging branches with their backs and rumps and deposition of faeces along trails may be a means of olfactory communication used in the maintenance of territories (Wells 1972, 1978a; McIlroy 1973; Gaughwin 1981). Detailed descriptions of individual behaviours are available for the Southern Hairy-nosed Wombat (Wunschmann 1966, 1967, 1970; Gaughwin 1981) and the Common Wombat (Böer 1980).

The highest levels of wombat activity occur in the mating season and are often accompanied by a marked increase in vocalisations. Common Wombats appear to have a larger repertoire of vocalisations (McIlroy 1973) than Southern Hairy-nosed Wombats (Gaughwin 1981). The most common vocalisation in both genera is a harsh cough which can become more strident when the animal is alarmed. In the Southern Hairy-nosed Wombat, the 'coughs' are short, 150–300 msec at 1–8 kHz, with most energy in the 2–3 kHz range (Gaughwin 1981). In any social interaction the call is given by the 'responder' animal. Calls often are emitted by oestrous females when pursued by males or, less frequently, by subordinate males in male-male encounters. Fighting, although rare, does occur and consists of bites to ears, rump and flanks.

Wombat energetics and thermoregulation are closely linked to behaviour. Wombats generally emerge to feed at night when the air temperature outside their burrows is equal to, or more often less than that within the burrows. In this way, they avoid high ambient temperatures (McIlroy 1973; Wells 1973, 1978b). This behaviour is of particular importance to the Southern Hairy-nosed Wombat, as above ground behaviour shifts to the period before dawn in summer and serves to conserve water that would otherwise be lost in thermoregulation. In winter, above ground behaviour tends to occur in the early evening before temperatures have dropped and serves to conserve energy (Well 1978b).

Economic Significance

Wombats only become a problem to man when fences are constructed across their trails, crops are grown adjacent to their burrows or highways are built through the middle of their habitat. Where studied, the economic impact of the Southern Hairy-nosed Wombat on crops has been shown to be minimal (Tiver 1980, 1981). Their impact on fences can be alleviated by building heavily weighted swing gates (B. Coman, personal communication). The problem of road kills has no single solution as highways act as watersheds, providing green pick along their verges during summer, thereby attracting both wombats and kangaroos. Elimination of populations along highways provides only temporary alleviation as these areas eventually will be recolonised.

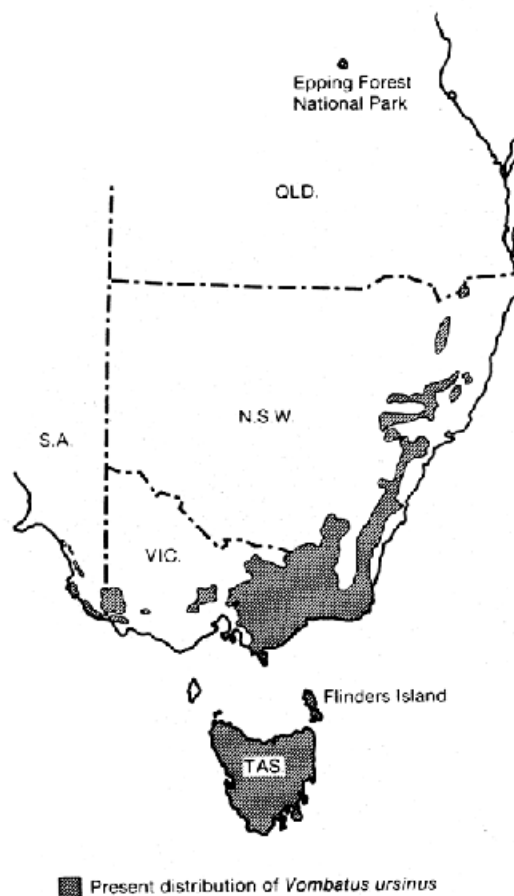
In the more arid areas, wombat warrens are often colonised by rabbits. Early attempts at rabbit eradication involving fumigation and ripping of burrows may well have led to the extinction of many wombat populations (Mallett & Cooke 1986). Wombats are now protected by legislation. Effective management of wombat populations awaits the development of a more accurate means of assessing their numbers and status. (McIlroy 1976; Wells 1978a).

BIOGEOGRAPHY AND PHYLOGENY

Distribution

McIlroy (1973) and Mallett & Cooke (1986) provided detailed information on the distribution of the Common Wombat (Fig. 32.9). Aitken (1971a) and Tiver (1980, 1981) have mapped the distribution of the Southern Hairy-nosed Wombat (Fig. 32.8) and Wilkinson (1979) the distribution of the Northern Hairy-nosed Wombat, *L. krefftii* (Fig. 32.9).

Figure 32.9 Distribution of *Vombatus ursinus*. (After McIlroy 1973; Mallett & Cooke 1986). *Lasiorchinus krefftii* is confined to the Epping Forest National Park, Queensland. (After Gordon & Wilkinson 1979)



Affinities with other Groups

Archer (1984b) discussed the question of marsupial phylogeny. Wombats share more synapomorphies with koalas than any other group. These include similarities in serology, cytology, sperm morphology, dental and basicranial features. These affinities notwithstanding, the morphological divergence between these families points to a separation in the early Tertiary. Archer (1984b) grouped koalas and wombats in the superfamily Vombatoidea which includes thylacoleonids, diprotodontids and palorchestids (Fig. 32.10)

Affinities within the Vombatidae

Archer (1984b) summarised the current understanding of relationships within the taxon in a cladogram and lists the relevant synapomorphic features (Fig. 32.11).

Fossil Record

The fossil record of wombats is largely confined to the late Pliocene and Pleistocene and, as detailed above, is inextricably intertwined with the discovery and naming of the living species. Only *Rhizophascolonus crowcroftii* has rooted

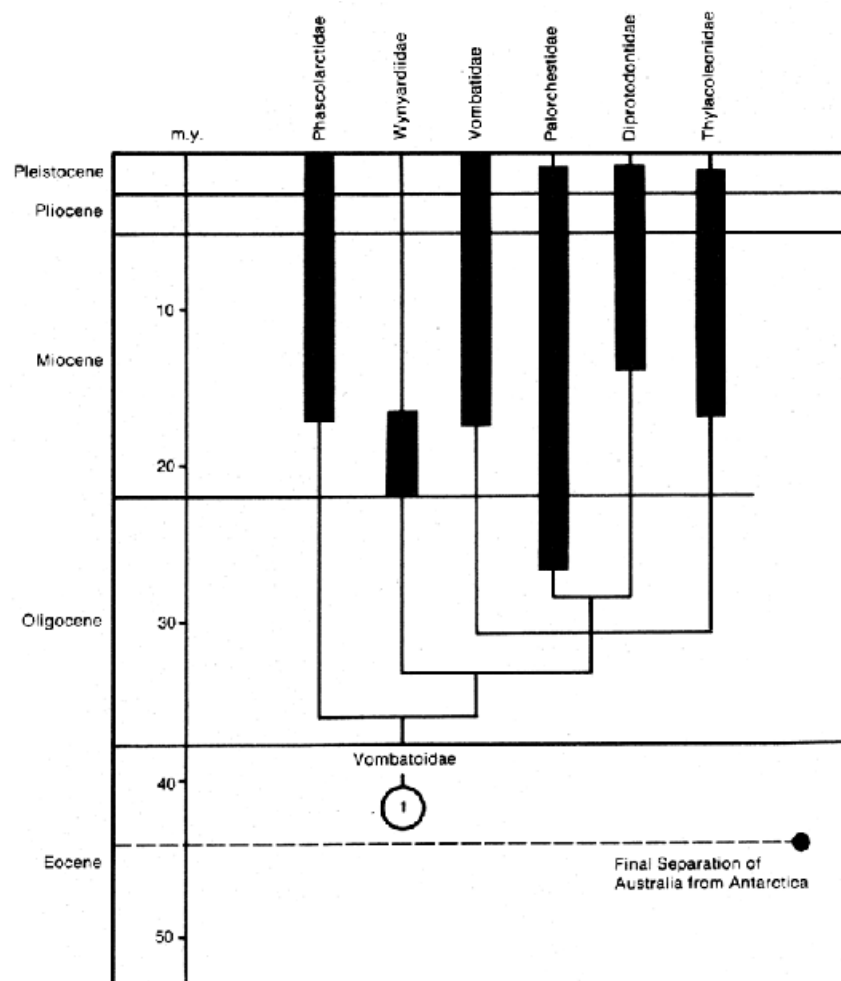


Figure 32.10 Cladogram showing relationships within the superfamily Vombatoidea. (After Archer 1984b). Synapomorphic features linking members of the superfamily are: I2 is lost, the paraflocculus of the brain is reduced in prominence, the brains are ovoid in shape and gyrencephalic, the head of the spermatozoan has a prominent hook, living members exhibit serological affinity, a cardiogastric gland patch in the stomach, a compact pancreas.

cheek teeth, suggesting a radiation of the open rooted grazing forms in the late Tertiary or Pleistocene, which parallels similar evolution of the grazing kangaroos and the spread of grasslands across the continent (Martin 1984). During this period, wombat populations probably achieved their greatest spread. *Vombatus* species occupied the coastal margins and ranges from southwestern Western Australia (Glauert 1912) to the Darling Downs of Queensland (Woods 1960b) and across Bass Strait to Tasmania. The past distribution of *Lasiorhinus* parallels that of *Vombatus*, but covers drier country further inland. It has been found as fossils from Balladonia in Western Australia (Glauert 1912), Lake Menindee, New South Wales (Tedford 1955) to the Darling Downs of Queensland (De Vis 1891). This period marked a change to a drier, more seasonal climate. By late Pleistocene times, the Australian climate was characterised by cold, dry, windy conditions (Galloway & Kemp 1984). This period marked the last appearance of many fossils with the range of living species contracting to that at the time of European settlement.

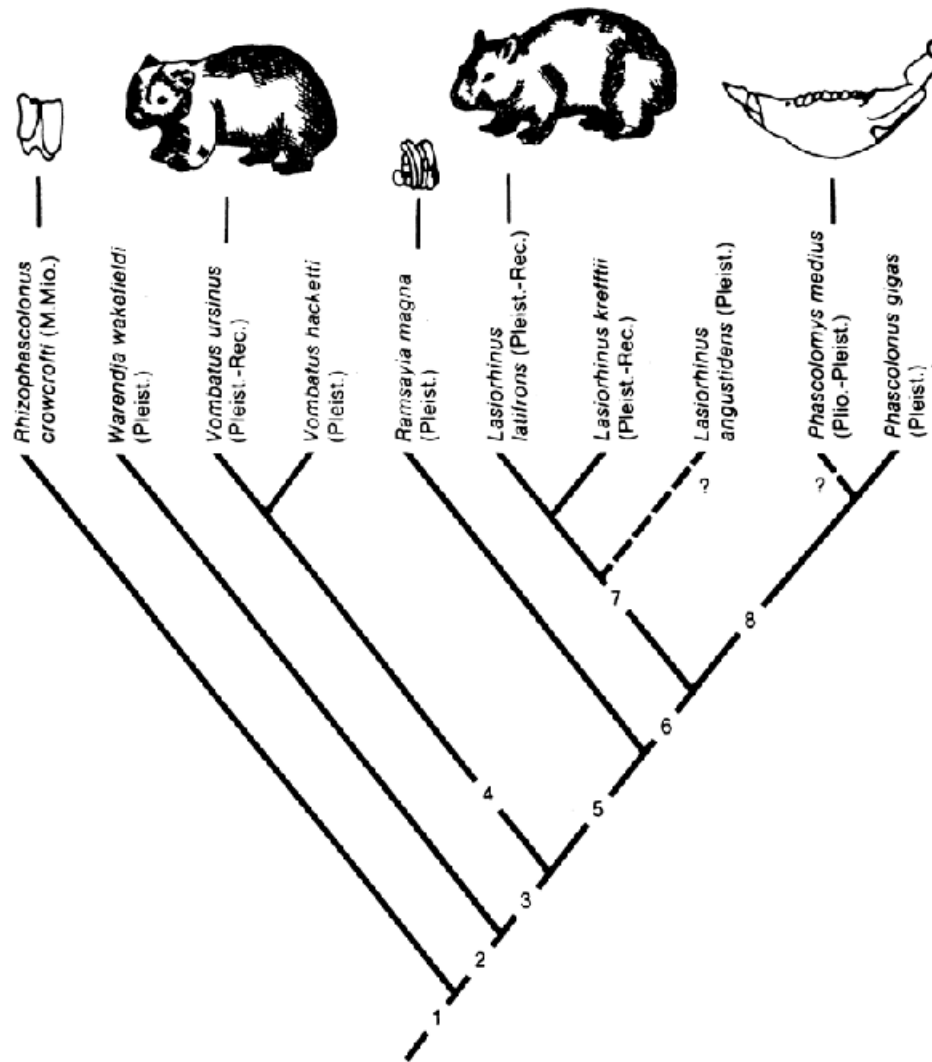


Figure 32.11 A cladogram showing possible relationships among the Vombatidae. (After Archer 1984b). Synapomorphic features are (1). loss of I2 and I3, molars formed into two pillar structures; (2). loss of roots on molars; (3). deep dentary and narrow ascending ramus, markedly curved molars; (4). features of nasal region, enamel of I1 surrounds the buccal surface; (5). incisive foramina converge posteromedially; (6). anterior end of palate flared; (7). features of nasal region, enamel of I1 confined to distal part of buccal surface, incisive foramina diverge posteriorly; (8). P3 is subrectangular in transverse section, a V shaped cleft occurs in the anterior end of the palate and I1 is very broad.

COLLECTION AND PRESERVATION

Collection

Wombats are best collected by trapping cages set in the burrow entrance (McIlroy 1976; Wells 1978a). Trapping success is greatest during the breeding season.

Wombats are tranquilised easily with Diazepam. Low doses (10 mg per animal) induce light sleep and muscle relaxation in *Lasiorhinus* species (Gaughwin 1982). Ketalar (100 mg/ml) mixed in equal portions with Rompum (20 mg/ml) and administered at 0.1 ml/kg body weight induces anaesthetic coma within 10 minutes, lasting 20–40 minutes with full recovery in 12 hours (D. Schultz, personal communication).

LITERATURE CITED

- Aitken, P.F. (1971a). The distribution of the Hairy-nosed Wombat [*Lasiorhinus latifrons* (Owen)] Part 1: Yorke Peninsula, Eyre Peninsula, the Gawler Ranges and Lake Harris. *South Australian Naturalist* 43: 93-103
- Angus, G.F. (1861). Notes on the broad-fronted wombat of South Australia (*Ph. latifrons* Owen). *Proceedings of the Zoological Society of London* 1861: 268-271
- Archer, M. (1984b). The Australian marsupial radiation. Pp. 633–808 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- Arvy, L. (1973). L'appendice vermiforme ou caecal. Pp. 727-728 in Grassé, P.-P. (ed.) *Traité de Zoologie. Mammifères*. Masson et Cie : Paris Tom. XVI
- Boardman, W. (1943). On the external characters of the pouch young of some Australian marsupials. *Australian Zoologist* 10: 138-160
- Böer, M. (1980). Beitrag zur Biologie der Plumpbeutler (Vombatidae) und zum Verhalten von *Vombatus ursinus* Shaw, 1800 in Zoologischen Garten. Unpubl. PhD Thesis, Hannover, Tierärztliche Hochschule 106 pp.
- Brooks, D.E., Gaughwin, M. & Mann, T. (1978). Structural and biochemical characteristics of the male accessory organs of reproduction in the Hairy-nosed Wombat (*Lasiorhinus latifrons*). *Proceedings of the Royal Society of London B* 201: 191–207
- Conder, P. (1970). Breeding the common wombat in captivity. *Victorian Naturalist* 87: 322
- Crandall, L.S. (1973). *The Management of Wild Animals in Captivity*. University Chicago Press : Chicago 100 pp.
- Crossman, D.G. & Gordon, G. (1986). The Northern Hairy-nosed Wombat *Lasiorhinus krefftii* (Owen). *Australian Mammal Society Bulletin* 9(1): supplement [Abstract]
- Crowcroft, P. (1967). Studies on the Hairy-nosed Wombat *Lasiorhinus latifrons* (Owen, 1845) 1. Measurements and taxonomy. *Records of the South Australian Museum* 15: 383-398
- Darden, T.R. (1972). Respiratory adaptations of a fossorial mammal, the pocket gopher (*Thomomys bottae*). *Journal of Comparative Physiology* 78: 121-137
- Dawson, L. (1981). The status of the taxa of extinct giant wombats (Vombatidae : Marsupialia), and a consideration of vombatid phylogeny. *Australian Mammalogy* 4: 65-79
- Dawson, L. (1983a). The taxonomic status of small fossil wombats (Vombatidae : Marsupialia) from Quaternary deposits, and of related modern wombats. *Proceedings of the Linnean Society of New South Wales* 107: 101-123
- Dawson, L. (1983b). On the uncertain generic status and phylogenetic relationships of the large extinct vombatid species *Phascolomys medius* Owen, 1872 (Marsupialia : Vombatidae). *Australian Mammalogy* 6: 5-13
- Dawson, T.J. & Hulbert, A.J. (1970). Standard metabolism, body temperature and surface areas of Australian marsupials. *American Journal of Physiology* 218: 1233–1238
- De Vis, C.W. (1891). Remarks on post-Tertiary Phascolomyidae. *Proceedings of the Linnean Society of New South Wales* 2: 235-246
- Dierenfeld, E.S. (1984). Diet quality of sympatric wombats, kangaroos and rabbits during severe drought. Unpubl. PhD Thesis, Ithaca, Cornell University 191 pp.

- Doube, L.J. (1981). Diseases of wombats. Pp. 63-75 in Fowler, M.E. (ed.) *Wildlife Diseases of the Pacific Basin and Other Countries*. Proceedings of the 4th International Conference of the Wildlife Disease Association. Sydney
- Dukes, H.H. (1955). *The Physiology of Domestic Animals*. Cornell University Press : Ithaca 1920 pp.
- Flower, S.S. (1931). Contributions to our knowledge of the duration of life in vertebrate animals. V. Mammals. *Proceedings of the Zoological Society of London* 1931: 145-234
- Foster, A.B., Hume, I.D. & Barboza, P.S. (1986). Nitrogen metabolism in the common wombat (*Vombatus ursinus*). *Australian Mammal Society Bulletin* 9(1): 32 [Abstract]
- Fraenkel, L. (1905). Vergleichend histologische Untersuchungen über das Vorkommen drüsiger Formationen im interstitiellen Eierstockgewebes (glande interstitielle de l'ovaire). *Archives für Gynaekologie* 175: 443-507
- French, R. (1965). Water resorption by the wombat hindgut. Unpublished Zoology Honours Thesis, Adelaide : University of Adelaide 35 pp.
- Galloway, R. & Kemp, E. (1984). Late Cainozoic environments in Australia. Pp. 83-95 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography and Evolution in Australasia*. (*Animals in Space & Time*). Hesperian Press : Carlisle
- Gaughwin, M.D. (1981). Socio-ecology of the Hairy-nosed Wombat (*Lasiornhinus latifrons*) in the Blanche Town region of South Australia. Unpublished PhD Thesis, Adelaide, University of Adelaide 137 Pp.
- Gaughwin, M.D. (1982). Southern Hairy-nosed Wombat *Lasiornhinus latifrons*: its maintenance, behaviour and reproduction in captivity. Pp. 145-155 in Evans, D.D. (ed.) *The Management of Australian Mammals in Captivity*. Zoological Parks Board of Victoria : Melbourne
- Glauert, L. (1912). Fossil marsupial remains from Balladonia in the Eucla Division. *Records of the Western Australian Museum* 1: 47-65
- Gordon, G. & Wilkinson, G. (1979). Conservation measures for the Queensland Hairy-nosed Wombat [*Lasiornhinus barnardi* (Longman)]. Submission by Queensland National Parks & Wildlife Service to World Wildlife Fund, Australia 9 pp.
- Gowland, P.N. (1973). Aspects of the digestive physiology of the common wombat *Vombatus ursinus* (Shaw, 1800). Unpubl. Zoology Honours Thesis, Canberra : Australian National University 87 pp.
- Green, R.H. (1973). *The Mammals of Tasmania*. Mary Fisher Bookshop : Launceston xv 76 pp. [27]
- Haight, J.R. & Murray, P.F. (1981). The cranial endocast of the Early Miocene marsupial *Wynyardia bassiana* : An assesment of taxonomic relationships based upon comparison with recent forms. *Brain, Behaviour and Evolution* 19: 17-36
- Hill, W.C.O. & Rewell, R.E. (1954). The caecum of monotremes and marsupials. *Transactions of the Zoological Society of London* 28: 185-240
- Hingson, D.H. & Milton, G.W. (1968). The mucosa of the stomach of the wombat *Vombatus hirsutus* with special reference to the cardiogastric gland. *Proceedings of the Linnean Society of New South Wales* 93: 69-75
- Hughes, R.L. (1965). Comparative morphology of spermatozoa from five marsupial families. *Australian Journal of Zoology* 13: 533-543
- Johnson, J.I., Haight, J.R. & Megirian, D. (1973). Convolutions related to sensory projections in the cerebral neocortex of marsupial wombats. *Journal of Anatomy* 114: 153

- Jones, F. Wood (1924). *The Mammals of South Australia*. Part II Government Printer : Adelaide pp. 133-270
- Kershaw, J.A. (1909). Notes on the hairy-nosed wombat *Phascolomys latifrons* Owen. *Victorian Naturalist* 26: 118-119
- Knox, R. (1826). On the wombat of Flinders. *Edinburgh New Philosophical Journal* 1: 104-111
- Krefft, G. (1872). Letter to Dr. Sclater on wombats. *Proceedings of the Zoological Society of London* 1872: 795-796
- Lee, C.S. & O'Shea, J.D. (1977). Observations on the vasculature of the reproductive tract in some Australian marsupials. *Journal of Morphology* 154: 95-114 [17]
- Lönnberg, E. (1902). On some remarkable digestive adaptations in diprotodont marsupials. *Proceedings of the Zoological Society of London* 1902: 12-31
- Lydekker, R. (1891). On the generic identity of *Sceparnodon* and *Phascolonus*. *Proceedings of the Royal Society of London* 59: 60-64
- MacKenzie, W.C. (1918b). *The Liver, Spleen, Pancreas, Peritoneal Relations, and Biliary System in Monotremes and Marsupials*. Critchley Parker : Australia xv 157 pp.
- MacKenzie, W.C. & Owen, W.J. (1919a). The genito-urinary system in monotremes and marsupials Pp. 1-106 in, *The Comparative Anatomy of Australian Mammals*. Part IV Plenum Press : New York
- Mallett, K.J. & Cooke, B.D. (1986). *The Ecology of the Common Wombat in South Australia*. Nature Conservation Society of South Australia : Adelaide 55 pp.
- Martin, H. (1984). Australian phytogeography. Pp. 17-30 in Archer, M. & Clayton, G. (eds) *Vertebrate Zoogeography & Evolution in Australasia. (Animals in Space & Time)*. Hesperian Press : Carlisle
- McIlroy, J.C. (1973). Aspects of the ecology of the common wombat *Vombatus ursinus* (Shaw 1800). Unpublished PhD Thesis, Canberra : Australian National University xvi 285 pp.
- McIlroy, J.C. (1976). Aspects of the ecology of the Common Wombat, *Vombatus ursinus* I. Capture, handling, marking and radio-tracking techniques. *Australian Wildlife Research* 3: 105-116
- Merrilees, D. (1967). Cranial and mandibular characteristics of modern mainland wombats (Marsupialia : Vombatidae) from a palaeontological view point, and their bearing on the fossils called *Phascolomys parvus* by Owen (1872). *Records of the South Australian Museum* 15: 399-418
- Milton, G.W., Hingson, D.J. & George, E.P. (1968). The secretory capacity of the stomach of the wombat *Vombatus hirsutus* and the cardiogastric gland. *Proceedings of the Linnean Society of New South Wales* 93: 60-88
- Mitchell, P.C. (1916). Further observations on the intestinal tract of mammals. *Proceedings of the Zoological Society of London* 1916: 183-252
- Murie, P. (1865). On the identity of the Hairy-nosed Wombat (*Phascolomys lasiorhinus* Gould) with the Broad-nosed Wombat (*P. latifrons* Owen) with further observation on the several species of this genus. *Proceedings of the Zoological Society of London* 1865: 834-854
- Newsome, A.E., Catling, P.C. & Corbett, L.K. (1983b). The feeding of the dingo *Canis familiaris dingo* 2. Dietary and numerical relationships with fluctuating prey populations in southeastern Australia. *Australian Journal of Ecology* 8: 345-366
- Nicholson, P.J. (1963). Wombats. *Timbertop Magazine* 8: 32-38

- O'Donoghue, C.H. (1916). On the corpora lutea and interstitial tissue of the ovary in the Marsupialia. *Queensland Journal of Microscopical Science* 61: 433-473
- Owen, R. (1836). Notes on the anatomy of the wombat. *Proceedings of the Zoological Society of London* 1836: 49-53
- Owen, R. (1868). *On the Comparative Anatomy and Physiology of Vertebrates. Vol.3.* Longmans Green : London 915 pp.
- Owen, R. (1877). *Researches on the Fossil Remains of the Extinct Mammals of Australia*; with a notice of the extinct marsupials of England. (pp. 297-299 *Phascolomys*) Vol. 1. J. Erxleben : London 522 pp.
- Pearson, J. (1944). The female urogenital system of the Marsupialia with special reference to the vaginal complex. *Papers and Proceedings of the Royal Society of Tasmania* 1944: 71-98
- Presidente, P.J.A. (1982b). Common wombat *Vombatus ursinus*: maintenance in captivity, blood values, infectious and parasitic diseases. Pp. 133-143 in Evans, D.D. (ed.) *The Management of Australian Mammals in Captivity*. Zoological Parks Board of Victoria : Melbourne
- Sanderson, K.J. & Pearson, L.J. (1981). Retinal projections in the hairy-nosed wombat, *Lasiorninus latifrons* (Marsupialia: Vombatidae). *Australian Journal of Zoology* 29: 473-482 [17]
- Sonntag, C.F. (1922). On the myology and classification of the wombat, koala and the phalangiers. *Proceedings of the Zoological Society of London* 1922: 863-896
- Stirling, E.C. (1913). Fossil remains of Lake Callabonna. 2. On the identity of *Phascolomys* (*Phascolonus*) *gigas* Owen and *Sceparnodon ramsayi* Owen; with a description of some of its remains. *Memoirs of the Royal Society of South Australia* 1: 127-178 18 pls
- Stirling, E.C. & Zietz, A.H. (1899). Preliminary notes on *Phascolonus gigas* Owen and its identity with *Sceparnodon ramsayi* Owen. *Transactions of the Royal Society of South Australia* 1: 123-135
- Stirton, R.A., Tedford, R.H. & Woodburne, M.O. (1967). A new Tertiary formation and fauna from the Tirari Desert, South Australia. *Records of the South Australia Museum* 15: 427-62
- Strezlecki, E. (1974). Physiological and behavioural aspects of thermoregulation in the Common Wombat *Vombatus ursinus* (Shaw). Unpublished Biology Honours Thesis, Flinders University : Adelaide 60 pp.
- Tancred, E. (1981). The distribution and sizes of ganglion cells in the retinas of five Australian marsupials. *Journal of Comparative Neurology* 196: 585-604 [17]
- Tate, G.H.H. (1951c). The wombat (Marsupialia, Phascolomyidae). *American Museum Novitates* 1525: 1-18
- Tedford, R.H. (1955). Report on the extinct mammalian remains at Lake Menindee, N.S.W. *Records of the South Australian Museum* 11: 299-305
- Tiver, P.J. (1980). Distribution and abundance of the Hairy-nosed Wombat *Lasiorninus latifrons* and its impact on the rural industry in the Fowler's Bay area. Unpublished report prepared for and funded by the National Parks and Wildlife Service, Department of Environment & Planning, South Australia 46 pp.
- Tiver, P.J. (1981). Hairy-nosed Wombats (*Lasiorninus latifrons*) in the Murray Lands. Unpublished report prepared for and funded by the National Parks and Wildlife Service Department of Environment & Planning, South Australia 43 pp.

- Triggs, B., Brunner, H. & Cullen, J.M. (1984). The food of fox, dog, and cat in Croajingalong National Park, south-eastern Victoria. *Australian Wildlife Research* 11: 491-499
- Troughton, E. le G. (1941). *Furred Animals of Australia*. Angus & Robertson : Sydney 1st edn 374 pp.
- Trumble, H.C. (1948). Rainfall, evaporation and drought frequency in South Australia. *South Australia Journal of Agriculture* 52: 55-64
- Wade, O. (1968). Structural characteristics of the heart of the wombat *Lasiorhinus latifrons*. *American Midland Naturalist* 80: 268-268
- Wakefield, N.A. (1961). Along the by-ways. Trees that animals like. *Victorian Naturalist* 78: 36-37
- Wakefield, N.A. (1967b). *Naturalists Diary*. Longmans : Melbourne 214 pp.
- Wells, R.T. (1968). Some aspects of the environmental physiology of the Hairy-nosed Wombat [*Lasiorhinus latifrons* (Owen)]. Unpublished Zoology Honours Thesis, University of Adelaide : Adelaide 35 pp.
- Wells, R.T. (1973). Physiological and Behavioural Adaptations of the Hairy-nosed Wombat (*Lasiorhinus latifrons*) (Owen) to its Arid Environment. Unpublished PhD Thesis, University of Adelaide : Adelaide
- Wells, R.T. (1978a). Field observations of the hairy-nosed wombat [*Lasiorhinus latifrons* (Owen)]. *Australian Wildlife Research* 5: 299-303
- Wells, R.T. (1978b). Thermoregulation and activity rhythms in the Hairy-nosed Wombat *Lasiorhinus latifrons* (Owen) (Vombatidae). *Australian Journal of Zoology* 26: 639-51
- Wells, R.T. (1984). Southern Hairy-nosed Wombat *Lasiorhinus latifrons*. p. 120 in Strahan, R. (ed.) *The Australian Museum Complete Book of Australian Mammals*. The National Photographic Index of Australian Wildlife. Angus & Robertson : Sydney
- Wells, R.T., Boreland, F. & Forward, L. (1986). The Brookfield Herbivore Study - grazing behaviours and pasture dynamics in a semi-arid zone. *Australian Mammal Society Bulletin* 9(1): unpaginated supplement [Abstract]
- Wilkinson, G. (1979). Conservation measures in the Queensland Hairy-nosed Wombat *Lasiorhinus barnardi* (Longman). Submission by Queensland National Parks and Wildlife Service to World Wildlife Fund, Australia
- Withers, P.C. (1972). Physiological adaptations of the Hairy-nosed Wombat, *Lasiorhinus latifrons*, to its fossorial habit. Unpubl. Zoology Honours Thesis, University of Adelaide : Adelaide 35 pp.
- Woods, T.J. (1960b). Fossiliferous fluvial and cave deposits. Pp. 393-403 in Hill, D. & Denmead, A.K. (eds) *The Geology of Queensland*. Melbourne University Press : Melbourne
- Wünschmann, A. (1966). Einige Gefangenschaftsbeobachtungen an Breitstirn - Wombats (*Lasiorhinus latifrons* Owen, 1845). *Zeitschrift für Tierpsychologie* 23: 56-71
- Wünschmann, A. (1967). Haltungserfahrungen mit Wombats. *Zoologischen Garten N.F., Jena* 34: 251-263
- Wünschmann, A. (1970). *Die Plumpbeutler (Vombatidae)*. (Die Neue Brehm-Bücherei, 421). Ziemsen : Wittenberg-Lutherstadt 83 pp.