



FAUNA *of* AUSTRALIA

31. PHASCOLARCTIDAE

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Koala—*Phascolarctos cinereus* [CSIRO Wildlife & Ecology]

DEFINITION AND GENERAL DESCRIPTION

The family Phascolarctidae contains one extant species, the Koala, *Phascolarctos cinereus* (Goldfuss), and five extinct species grouped into four genera, including *Phascolarctos*. All are confined to Australia.

The Koala shares a suite of characters with the vombatids (wombats) which distinguishes the two taxa from other Australian diprotodont marsupials: the pouch opens towards the back rather than the front; they possess cheek pouches and a vestigial tail; neither possess the first and the second premolars; the palatine vacuities are restricted to the palatines rather than extending beyond their boundaries; the symphysis of the lower jaw is fused; the ventral arch of the axis vertebra consists of cartilage rather than bone; the transverse process of the seventh cervical vertebra is perforate; the supratragus of the ear is small; they possess a distinctive gastric gland; there is no cleido-occipital muscle; the omotrachelian muscle is single rather than double and the pericardium adheres to the diaphragm, rather than being connected by membranous sheets.

In contrast to the vombatids, which have a single incisor on either side of the upper jaw and rootless persistently growing teeth, the Koala has three incisors on either side of the upper jaw and teeth with roots. Its skull is deep and straight-sided, in contrast to the exceptionally broad and dorsoventrally compressed skull of vombatids (Fig. 31.1). It also may be distinguished by the shape of the manus. This is forcipate in the Koala, with digits I and II opposed to the remainder; each digit terminates in a strongly recurved claw (Fig. 31.2). The manus of vombatids is spatulate and the digits terminate in claws which are long, but straight. the Koala has only six or seven caudal vertebrae in contrast to the 12 to 13 caudals present in vombatids.

HISTORY OF DISCOVERY

Curiously, such a large and conspicuous marsupial as the Koala escaped mention in historical records until 1798, when John Price, a servant of Governor Hunter, referred in his journal to an animal 'which the natives called a cullawine, which much resembles the sloths in America' (cited in Iredale & Whitley 1934, p. 62). The first specimens, the feet of a dismembered Koala, were obtained by Ensign F. Barralier in 1802 and sent to Governor King. Barralier referred to the collection of these specimens in his journal:

'Gory told me that they had brought portions of a monkey (in the native language Colo), but they had cut it into pieces, and the head, which I should have liked to secure, had disappeared. I could only get two feet through an exchange which Gory made for two spears and one tomahawk. I sent these two feet to the Governor preserved in a bottle of brandy' (cited in Iredale & Whitley 1934, p. 62).

The following year, Barralier obtained a live animal for the Governor and a description appeared in the Sydney Gazette of August 21, 1803:

'An animal whose species was never before found in the Colony is in His Excellency's possession. When taken, it had two Pups, one of which died a few days since. This creature is somewhat larger than the Waumbat and although it might at first appearance be thought much to resemble it, it nevertheless differs from that animal. The fore and hind limbs are about of equal length, having sharp talons at each extremity, with which it must have climbed the highest trees with much facility. The fur that covers it is soft and fine and of a mixed grey colour; the ears are short and open; the graveness of the visage, which differs little in colour from the back, would seem to indicate a more than ordinary

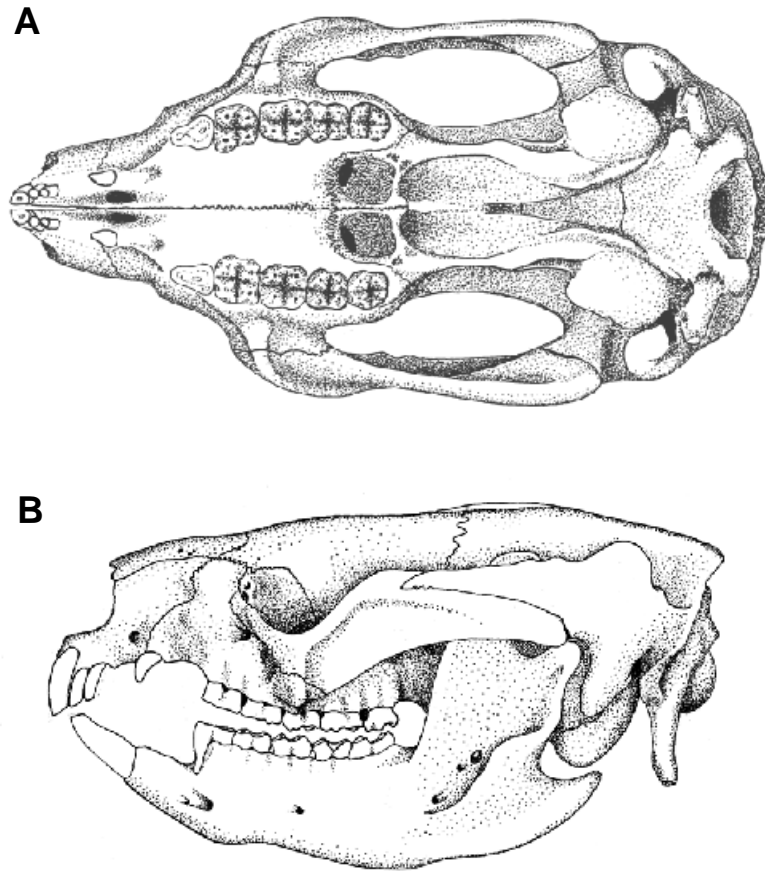


Figure 31.1 **A**, Ventral; **B**, lateral views of the skull of *Phascolarctos*. Scale
 X 0.57. (© ABRS) [H. Heinrich]

portion of animal sagacity; and the teeth resemble those of a rabbit. The surviving Pup generally clings to the back of the mother, or is caressed by her with a serenity that appears peculiarly characteristic; it has a false belly like the opossum, its food consists solely of gum leaves, in the choice of which it is excessively nice' (cited in Whitley 1975, p. 49).

The first detailed description was published by Home (1808), based on an account furnished by Lieutenant-Colonel Paterson, then Lieutenant-Governor of New South Wales. Home (1808) refers to the Koala as another species of wombat. A more thorough account, accompanied by an illustration, appeared in Perry's *Arcana* in 1810 under the alternative names of Koalo or New Holland Sloth. This description has been republished by Mathews & Iredale (1912). The French naturalist de Blainville proposed the generic name *Phascolarctos* with a description of a specimen from New South Wales, published in 1816, and Goldfuss (1817) used the combination *Lipurus cinereus* with a description in Schreber's *Die Säugethiere*. Goldfuss (1820) renamed the genus *Morodactylus* and Lay (1825) proposed the name *Draximenus*, but neither received wide usage. Four taxa were subsequently proposed: *Phascolarctos fuscus* by Desmarest (1820), *P. flindersii* by Lesson (1827), *P. koala* by Griffith, Smith & Pidgeon (1825-1835) and *Koala subiens* by Burnett (1830), but all were subsequently synonymised with *P. cinereus*. Iredale & Troughton (1934) summarised the synonymy, and historical accounts of the discovery and description of *Phascolarctos* appeared in Mathews & Iredale (1912), Iredale & Whitley (1934), Grzimek (1972), Whitley (1975) and Strahan (1978).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The Koala is a medium to large marsupial, unique amongst Australian native mammals in that it is the only non-human occupant of the continent which is really a 'frontal' mammal, that is, it tends to have a face rather than a muzzle. The eyes are forwardly directed and the 'rhinarium' is large and apparently vertically oriented. There is a relatively high forehead and the animal is normally observed in an upright stance. This frontal expression may explain the empathy generated in most people for this animal (Morris 1977). Pocock (1921) described the lack of a 'true rhinarium' in this species in contrast to its closest living relatives, the vombatids. Pocock (1921) also drew attention to the virtual absence of a supertragus in the external ear, as in the vombatids, and argued that this is an important character establishing their affinity, in view of the constancy in the development of this ridge in many mammals. The stout form, thick woolly fur, large thickly furred ears and the rudimentary tail contribute to this animal's superficial resemblance to a small bear. This has led to its popular names of koala bear and native bear. A tail vestige can be observed upon close examination, although it commonly is supposed that this appendage is entirely absent (Le Souef, Burrell & Troughton 1926).

Sexual dimorphism is well developed in the Koala. Adult males can be up to 50% larger than adult females in the same population (Martin & Lee 1984). Males also have a prominent sternal gland, particularly conspicuous in the breeding season. Like most marsupials, the males of this species have a well-developed, pendulous scrotum situated cranial to the cloacal orifice. The pouch of females (described below) is usually not obvious unless it contains a developing pouch young.

Body Wall

As noted by Owen (1868) and more recently by Barbour (1977), the arrangement of the muscles of the body wall of marsupials is generally similar to the pattern found in eutherian mammals, except where the abdominal muscles are modified by their relationships to the epipubic bones. Martin (1836) and Owen (1868) believed that the epipubic bones of this species might be capable of a greater degree of abduction than in other marsupials. Sonntag (1922) noted the virtual absence of the quadratus lumborum muscle in the Koala and suggested that this is of some significance to the understanding of the relationships of the Phascolarctidae. The cutaneous musculature is well developed and there are virtually no subcutaneous fat deposits. Degabriele & Dawson (1979) examined the physiological properties of the integument of the Koala and found that the fur had the highest degree of insulation known for a marsupial in still air ($0.529^{\circ}\text{C} / \text{W} \times \text{m}^2$) and maintained a high insulative value in wind. The Meeh factor is reported to be 9.9 ± 0.5 (S.D.) and hair density (54.4 ± 3.1 hairs/mm²) on the dorsal body surface is double the value for the ventral surface. In contrast to the insulation values, the much paler ventral fur (52.3% reflectance) is better able to reflect solar radiation than the dorsal surface (38.3% reflectance). This combination of properties should allow the animal considerable flexibility in regulating heat balance with the environment by postural adjustments.

The pouch of female Koalas is a well-developed structure which assumes quite spacious proportions when occupied by a large pouch young. As in most marsupials, it is formed from the invagination of the skin through the cutaneous trunci muscle layer, whose fibres then form the sphincter marsupii. The hair and

glandular complement of the pouch skin differs from that of the general body surface and the single pair of mammary glands with its associated teats are found on the dorsal wall of the pouch. When not occupied by a large pouch young, the pouch has a central opening with well-developed lateral extensions into the groin on either side. As the young develops in the pouch, its increasing size distends the pouch wall in such a way that the pouch opening becomes distinctly backwardly directed. This would not seem to be a good arrangement for an animal that spends most of its time sitting or climbing in an upright stance in trees, but presumably most of the weight of larger pouch young is supported within the voluminous lateral extensions of the pouch. The arrangement of the pouch was described by Pocock (1921) and discussed in Strahan (1978).

Marshall, Carrick & Tolley (1988a) described the mammary apparatus of the Koala at the light and electron microscope level and proposed the term 'modified teat' to describe the part of the organ suckled by the developing pouch young. Marshall *et al.* (1988b) found that the composition of koala milk and the changes that occur during lactation are broadly comparable to the situation in other marsupials that have been studied.

Skeletal System

The most distinctive features of the phascolarctid skeleton are associated with the skull, the tail and the ribs. The rather box-like skull (Fig. 31.1) was aptly described by Thomas (1888, p. 209) as:

'oblong, parallel-sided, the zygomata running straight backwards from their broadest point at the orbits, not curved outwards. Nasals short and very broad, scarcely projecting in front beyond the ascending processes of the premaxillae. Interorbital region smooth and flat, its edges rounded, and forming rudimentary blunt post-orbital processes, supported in old age upon very large and smoothly rounded palatine vacuities and the prominence of the auditory bullae, which are very high and bear a superficial resemblance to the condition found in the pig'.

Sonntag (1922) argued forcefully for the separation of the Koala from the Phalangeridae, using the contrasting origins of the bullae (alisphenoid in the Koala and temporal in vombatids) as an indicator of the long separation of phascolarctids from the latter. Also in contrast to vombatids and, in fact, all other living marsupials with the exception of the Honey Possum, *Tarsipes rostratus*, this species exhibits virtually no inflection of the angle of the mandible (Abbie 1939a). The mandible also is fairly atypical of the phalangeroid condition in that the two halves are rather firmly fused together; this feature is shared with the vombatids.

A characteristic of marsupials is the high degree of uniformity in number of the presacral vertebrae. Jones (1923a) described the typical marsupial as having '7 joints in the neck, 13 joints and 13 ribs in the chest, 6 joints in the loins, and an indefinite number of joints in the tail'. The Koala is exceptional in having only 11 ribs, the smallest number reported for any Australian marsupial. The species also has the fewest caudal vertebrae: only six or seven rather than twice that number in vombatids, the only other group with a vestigial tail, and in contrast to the 20 to 30 caudal vertebrae common to the phalangeroids (Strahan 1978). Other unusual features of the axial skeleton of the Koala are the presence of perforations in the transverse processes of the seventh cervical vertebrae and the formation of part of the ventral arch of the axis from cartilage rather than bone (Sonntag 1922). Epipubic bones are very well developed and are readily palpable in the lower abdominal region.

Locomotion

The Koala is often viewed as a clumsy and sluggish creature, which clings to branches by its modified feet (see Sonntag 1922). This view is conditioned by the most common experience of the animal in captivity or occasional glimpses in the wild, which are mostly of individuals resting high up in trees during daylight hours. While the animal usually moves at a sedate pace, the proportionately very long limbs can propel the animal rapidly over the ground or up the trunks of small and very large trees alike. Koalas walk by moving the diagonally opposite limbs alternately and run by moving the forelimbs and then the hind limbs in unison. The extended digits and the palm adjacent to the digits touch the ground as does the entire hind foot, with the toes extended and the hallux held at right angles to the axis of the foot (Smith 1979a). When climbing, the hands are released with the arms extended and the body is thrust upwards by extending the hind limbs, permitting the hands to clasp at a new level (Smith 1979a). A description of the limb musculature of the Koala was provided by Sonntag (1922), although some care is required when making comparisons with modern descriptions of other mammals due to changes in terminology. The most distinctive features to emerge from this study are that no patella, even a cartilaginous one, is present; the deltoid muscle is completely undivided; the cleido-occipital muscle is absent and the 'omo-trachelian' muscle (presumably synonymous with the term omo-atlantic used in the body of his paper) has only a single insertion on the outer part of the spine of the scapula.

Carrick & Wood (1986) reported the efficacy of using an empirical 'Condition Index Score' (Table 31.1) based on the development of muscle masses on either side of the spine of the scapula. They found body weight a very ineffective index of general well-being of Koalas.

With the demise of the tail in ancestral phascolarctids, one of the characteristic adaptations of arboreal phalangeroids, a markedly prehensile tail, is precluded. The most obvious adaptations for arboreal locomotion in this species are the developments of the feet (Fig. 31.2). All digits except the broad hallux are equipped with large, strong, sharp and recurved claws. The syndactylous digits (II and III) on the pes are large, which Jones (1924) believed to be in harmony with the depth of the dense fur. The manus is very large and the first two digits are opposable to the other three, giving rise to a hand with two thumbs. Except for the apical pads, most of the palmar and plantar surfaces are granulated, rather than having striations or ridges and lack well-differentiated pads. The feet are described and illustrated by Pocock (1921) and Jones (1923a); more recently, Strahan (1978) considers the homologies and osteological features associated with the 'forcipate' condition of the manus.

In contrast to the phalangeroid pattern, Koalas never descend a tree or branch head first. Strahan (1978) suggested that the compact, stocky trunk with disproportionately long limbs may be an adaptation to leaping in a more or less upright posture. This is certainly a characteristic of the animal on those occasions when it leaps between adjacent branches.

Feeding and Digestive System

The Koala is one of the largest and most specialised of the arboreal folivores, feeding principally on the leaves of certain species of *Eucalyptus*, but also on shoots and soft stems (Smith 1979a) and even flowers and bark (Hindell, Handasyde & Lee 1985). Leaves are acquired by grasping stems with either forepaw and the apical foliage is sniffed as the stem is drawn to the mouth. If the stem is rejected, it is either firmly gripped in the incisors and held out of the way while another stem is grasped with a paw or *vice versa*. Leaves are stripped from a stem bearing acceptable foliage using the sharp longitudinal blades of the premolars. On this initial bite, the leaf is held diagonally across the mouth so

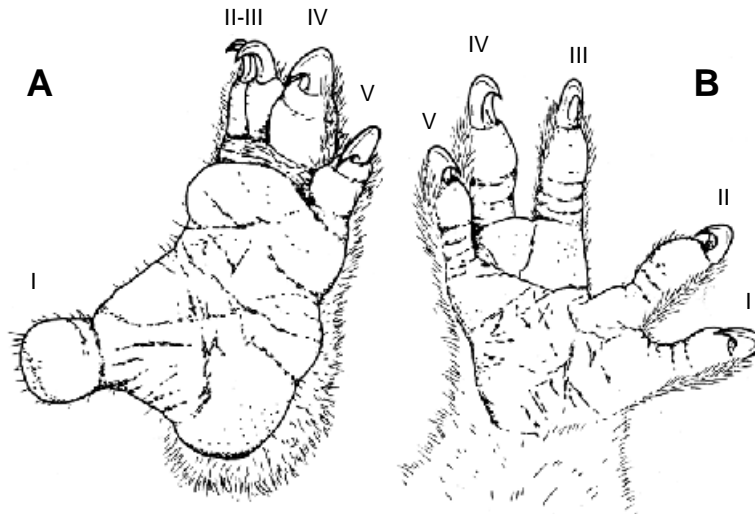


Figure 31.2 The left **A**, manus; **B**, pes of *Phascolarctos*. Scale $\times 0.41$.
(© ABRS) [D. Troon]

that the base of the leaf enters the premolars from a lingual direction. Mastication then commences with the leaf lying obliquely across the mouth (Lanyon 1982). Both young and mature leaves are ingested, but branches with only young leaves are stripped whereas only some of the leaves are removed from branches with solely mature leaves (Hindell *et al.* 1985). This is consistent with their preference for new growth in captivity (Fleay 1937; Pratt 1937; George 1977).

The morphology of the cheek teeth of the Koala has been described by Stirton (1957), Archer (1978c) and Strahan (1978). Lanyon & Sanson (1986a) reviewed these descriptions and described the occlusal relationships. The teeth are considered selenoid or subselenodont because of the long curved cristae originating from the four main cones (Fig. 31.3). In occlusion, the cristae shear past one another, with the lower teeth moving in an antero-lingual direction, leading to comminution of the fibrous leaf material (Lanyon & Sanson 1986a). The effect of tooth wear on comminution is described by Lanyon & Sanson (1986b).

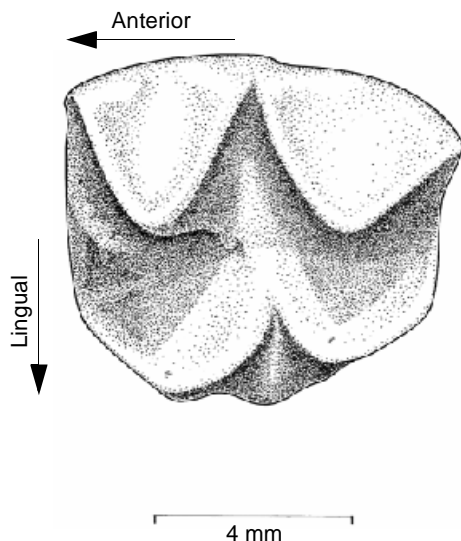


Figure 31.3 Occlusal surfaces of the cheek teeth of *Phascolarctos*. (© ABRS)
[G. Milledge]

The stomach is small in relation to the rest of the digestive tract (Fig. 31.4) and, with the exception of presence of the so-called gastric gland, bears no distinctive features. The gastric gland measures about 40 mm in diameter and lies distal to the oesophageal opening on the lesser curvature of the stomach. It contains 25 or so crypts which are presumed to secrete gastric juice into the lumen of the stomach (Harrop & Degabriele 1976, 1978).

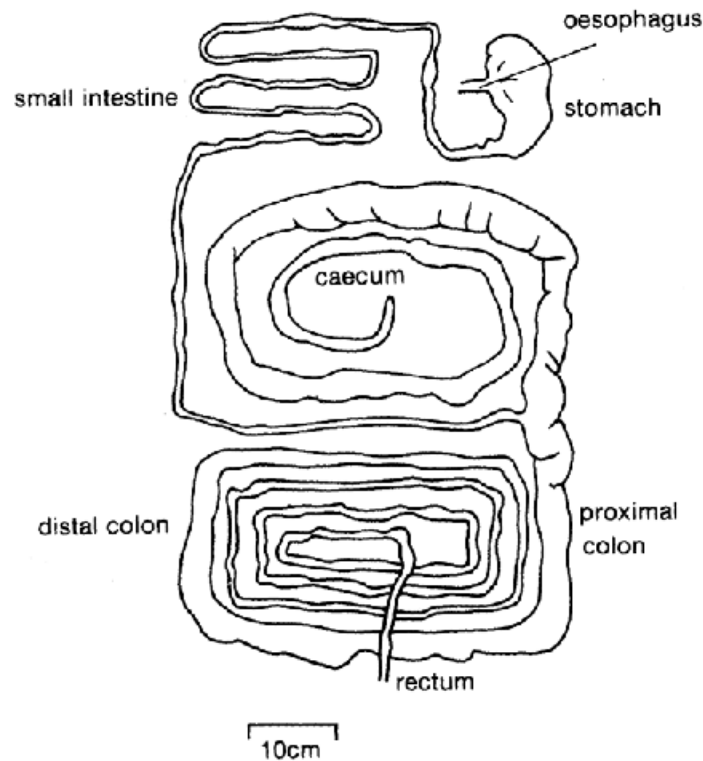


Figure 31.4 The digestive tract of *Phascolarctos* illustrating the relative proportions of components. (© ABRS) [K. Hollis]

The most notable feature of the alimentary tract of the Koala is the extraordinary development of the caecum, which MacKenzie (1918a) claimed is the longest and most capacious, in a relative sense, among mammals. In spite of its size, this structure, is not particularly specialised (Hill & Rewell 1954). Internally, the mucosa is smooth and is raised into 11 to 12 folds which run down its length into the proximal colon. The latter is also capacious and long, although only about half the length of the caecum, and continues into a much narrower distal colon, where faecal pellet formation occurs (Harrop & Degabriele 1976).

Until recently, it was assumed that the Koala possessed an alimentary tract typical of a non-ruminant mammalian herbivore with post-gastric fermentation. This assumption was based upon the size of the caecum relative to the stomach (MacKenzie 1918a; Sonntag 1921a; Harrop & Degabriele 1976, 1978). Cork, Hume & Dawson (1983), however, estimated that the total daily VFA production accounted for only 9% of the digestible energy intake. This suggested that digestion of cell contents rather than cell wall was the principal source of energy and that the enormous caecum has some function other than as a site for microbial digestion of plant fibre.

It now appears that digesta reaching the junction of the small intestine with the caecum and proximal colon is divided into two fractions; large particles pass down the proximal colon and are excreted rapidly, while the solute fraction and small particles are retained in the caecum and proximal colon (Cork & Warner 1983; Lanyon & Sanson 1986b). Cork & Warner (1983) obtained a mean retention time in the gut of 213 hours for solute phase markers compared with 99 hours for particulate markers. The fate of the solute and small particle phases in the caecum and proximal colon has yet to be ascertained, but their retention suggests a dependence on these phases and emphasises the importance of fine comminution of leaves by the teeth. Cork & Sanson (1988) reassessed the available information on digestive processes and concluded that the importance of the hind gut could be greater than indicated by those studies where *Eucalyptus punctata* was the principle dietary component. Osawa & Carrick (1988) showed that substantial aggregate changes occur in the faecal flora of Koalas in response to seasonal change, differing body condition and systemic antibiotic therapy. Their results suggest that certain elements of the intestinal microflora might play an important role in maintaining the integrity of digestive capability of koalas.

Circulatory System

The heart of the Koala is fairly typical of marsupials, and indeed of mammals. It is about 50 mm long and rounded at the apex, which is positioned level with the caudal border of the fourth left costal cartilage. As in most marsupials, right auricular extensions encompass the aorta and there is no trace of a fossa ovalis. The right atrioventricular valve appears to have one very large non-septal cusp. There is no obvious phrenicopericardiac ligament, so that the pericardium appears to be directly adherent to the diaphragm (Martin 1836; Owen 1868; Forbes 1881; Sonntag 1921a, 1922). Dickens (1975) reported a normal resting heart rate of 90 beats/min and Wood (1978) considered a pulse rate of 60–80 beats/min normal for captive animals.

The pattern of branching of the conducting arteries off the aortic arch appears to be quite variable in Koalas. In two specimens Forbes (1881) found one had a brachiocephalic trunk (from which the two carotids and the right subclavian artery branches) followed by the left subclavian, while the other had a brachiocephalic trunk contributing to the right subclavian and carotid, with separate origins of the left carotid and subclavian from the aorta. Martin (1836) found a pattern similar to this description. Sonntag (1921a), however, described the right subclavian, right common carotid and left common carotid as branching independently directly from the aorta in proximity to one another, to be followed shortly thereafter by the left subclavian. The origins of gonadal and iliac vessels from the abdominal aorta usually differ between the Marsupialia and Eutheria. This is seen also in the Koala. A common coeliacomesenteric arterial trunk is a feature of this species (Sonntag 1921a).

The most significant characteristic of the venous system in the Koala is the location of the caudal vena cava. It runs to the right of the abdominal aorta, and thus resembles the eutherian condition, rather than the pattern typical of marsupials in which the caudal vena cava runs ventral to and obscures the abdominal aorta (Sonntag 1921a). Dickens (1978a) compiled an extensive set of data on haematological parameters of the Koala from a number of geographical locations, thereby greatly extending the information provided by Bolliger & Backhouse (1960). It is normal to find small numbers of reticulocytes, cells containing Howell Jolly bodies and nucleated erythrocytes (Dickens 1978a). Anisocytosis and poikilocytosis also appear to be common in blood smears from this species. McFarlane *et al.* (1988a) extended the data on biochemical parameters of blood with reference to stress and infectious disease. Studies (McFarlane *et al.* 1988b) of coagulation and fibrinolytic parameters in koalas

indicated a very long mean prothrombin time (60.2 ± 11.6 sec) and inability of streptokinase to activate koala plasminogen. Clotting in Koalas, therefore, may differ from the pattern observed in eutherian mammals.

The spleen of the Koala is variable in shape and of all the Australian Marsupialia it conforms least to the forked pattern that is rather distinctive of the group (Martin 1836; Forbes 1881; MacKenzie 1918b).

Respiration

One of the most obvious and striking features of the Koala is its prominent nose. The external appearance, however, is deceptive and, in fact, the nasal cavity is quite small with the nasal conchae simple in form. Most of the space is taken up by large maxillary and frontal sinuses. There is no convincing demonstration of a specific function for paranasal sinuses even though they are common in mammals, so that the role of these prominently developed structures in this species remains intriguing.

Other distinctive features are the absence of swell bodies (thought to alternate air flow between right and left nasal passages in most mammals) and sparse development of secretory glandular tissues which normally modify the temperature and humidity of inspired air. Kratzing (1984a) suggested that the reduction of such tissues may be an adaptation contributing to water conservation in this species. Nevertheless, Degabriele & Dawson (1979) found that evaporative water loss, principally from the respiratory tract, is the main mechanism for maintenance of stable body temperature when this species is exposed to high ambient temperatures. They also reported that the resting respiratory rate of Koalas is 10–11 breaths/min, which can rise to 230 breaths/min when the animals are panting in response to elevated ambient temperatures; the ‘normal’ body temperature range is 35.5–36.5°C in unrestrained animals. Wood (1978) reported respiration rates in the range of 15–30 breaths/min and a body temperature of 36.7°C as normal for captive Koala. Dickens (1975) noted that pyrexias have not been observed and that ill Koalas generally exhibit hypothermia with temperatures as low as 29°C. Kratzing (1984b) also contrasted the absence of lateral nasal glands and maxillary sinus glands in Koalas with the prominence of these glands in three other marsupial species studied, and with the generally widespread occurrence of these glands in eutherians. Since it is known that the secretions of the lateral nasal glands are a source of immunoglobulin A for the respiratory epithelium in other mammals, the absence of these glands in the Koala may be of significance as a predisposing factor in the susceptibility of this species to infections of the respiratory system.

The arrangements of the nasopharynx in the Koala is unusual and the location of the larynx makes it quite difficult to insert an endotracheal tube to maintain anaesthesia in this species, since most laryngoscopes lack a sufficiently long blade. Dickens (1975) recommended holding the larynx externally to facilitate the process.

Sonntag (1921a) reported on the unusual caudal prolongation of the soft palate, which opens by quite a small orifice in close proximity to the oesophagus, more or less at right angles to the axes of the oesophagus and trachea. This arrangement makes it rather difficult to envisage how the large epiglottis functions and may be related to the habit in Koalas of stretching their neck back, so that the long axis of the head parallels that of the body, when making the bellowing grunt typical of males in the breeding season (Smith 1980a). The other vocalisation common in this species is the rather shrill cry most often heard from adult females or juveniles when alarmed or distressed and is usually uttered with the head at its normal perpendicular angle to the body.

Martin (1836) noted that the capacity of the thorax is very small in comparison to that of the abdomen and that the lungs are composed of three right lobes and two left lobes. Forbes (1881) confirmed this and noted that the lungs are simple in form, the right side having three and the left, two lobes. The lower lobes of each side are about equal in size, but half as big as the two upper lobes. Accessory lobes are not present. Sonntag (1921a), however, concluded that each lung contains two lobes.

Excretion

Martin (1836) and Sonntag (1921a) described the general arrangement of the urinary system. The kidneys are about 35 mm long, 20 mm wide and 15 mm thick, with the right kidney lying completely craniad to the left. Sonntag (1921a) also reported the occurrence of venous plexuses associated with the ureters and that the urinary bladder is typical of mammals. As in other marsupials, the kidney of this species is unilobar and has a single shallow papilla (Burger & Cross 1981).

Renal features which characterise this marsupial are the relatively wide cortex and outer medulla and the highly organised nature of the blood vessels and capillary networks in these regions. Medullary rays are very clearly defined. Interlobular vessels arise perpendicularly from the arcuates and follow straight paths to the capsule. Although this is a typical feature of mammalian kidneys, in most marsupials examined by Burger & Cross (1981) the arrangement of blood vessels is more haphazard. Glomerular and tubular dimensions are similar to other marsupials and proximal and distal tubules intertwine in tight convolutions close to the parent glomerulus. Although the renal papilla is shallow, loops of Henle traverse its full depth and the Koala can produce a urine that is more concentrated than that of Man, but less concentrated than is typical of rodents and carnivores.

Sense Organs and Nervous System

The eye in the Koala is unusual. The pupils are vertical slits rather than circular as in other marsupials.

In view of the observation that captive individuals sniff the petiole of many leaves before taking them into their mouths, it is surprising that the olfactory epithelium is not as extensive as that found in a range of other marsupials and no separate septal olfactory organ is present in this species (Kratzing 1984a). A vomeronasal organ with a patent duct system is present, but again, it is only moderately developed. This latter system is most likely involved with pheromonal signals associated with reproduction or social organisation, for example, the use of secretions of the sternal gland of male Koalas to mark trees. All sensory vibrissae are at best poorly developed.

Sonntag (1921a) describes the arrangement of the vagus and related nerves, including part of the abdominal sympathetic network. The exceptionally small size of the brain of the Koala, and especially the reduction in size and extreme smoothness of the cerebral hemispheres, has been remarked upon by several early authors and more recently by Haight (1981) and Haight & Nelson (1987). Not only are the cerebral hemispheres reduced in size so that they fail to cover much of the brain stem and are lissencephalic, but the brain is also some 25–30% smaller than the endocranium that houses it. The histological appearance, however, is much as one would expect.

Endocrine and Exocrine Systems

Ever since MacKenzie & Owen (1919b) speculated that there might be a relationship between what they termed ‘retrogression’ in the adrenal glands of the Koala (and brush-tail possums, *Trichosurus* species) and hypothetical hormonally active substances in their diet, it has been surmised that the species has an incipient adrenocortical insufficiency and that this has a causal relationship to the widely recognised susceptibility of Koalas to ‘stress’ (Butler 1978; Wood 1978; Obendorf 1983). Attempts to provide replacement therapy with exogenous corticosteroids were usually unsuccessful (Braysher 1978). Bolliger (1953) dismissed any link with adrenocortical hormone-like substances in the leaf diet and reported that the adrenals exhibited a histology typical of mammals. He did confirm, however, that the adrenals of this species are proportionately quite small: about 10 mm long, 8 mm wide and 5 mm deep, weighing about 0.25 g. The right gland is usually rather smaller than the left and concealed under lobes of the liver, more or less adherent to the caudal vena cava. The ratio of adrenal to body weight is thus about 0.006%, less than half that typical of mammals (data from males only).

Booth & Carrick (1988) reported that the adrenal gland of the Koala responds to the challenge of disease in the usual way: a broadening of the zona fasciculata, depletion of lipid in this zone and overall enlargement of the gland with frequent formation of cortical nodules. Even under maximal stimulation of neoplastic disease, however, the adrenal gland weight to body weight ratio of Koalas remains unusually low compared to other mammals. The peripheral blood of ‘minimally stressed koalas’ has almost no cortisol (<0.1 ng/ml), with fairly small amounts of corticosterone (0.7 ng/ml) and 11-deoxycortisol (0.1 ng/ml) (Scoggins 1978). In response to trophic stimulation, the major response is a dramatic increase in the amount of cortisol (7 ng/ml) in the circulation with comparatively minor increments in the other glucocorticoids. The mineralocorticoid detected in this species is aldosterone (0.06 ng/ml), which is comparable with the situation in other marsupials. Scoggins & Barlow (1981) extended the earlier study to include the effects of stressors such as capture, confinement and traumatic injury (again only males were studied) and noted that in previous studies there is no biochemical or histological evidence to support the diagnosis of adrenal insufficiency. They conclude that in comparison with other marsupials, the Koala appears to have low peripheral blood corticosteroid concentrations and a relatively poor response to acute stress and trophic stimulation. They also add that further experimentation is required to determine whether this relative lack of responsiveness is causally related to the morbidity and mortality associated with ‘Koala Stress Syndrome’. The situation is complex since it has been shown that the adrenal of the Koala secretes 21-deoxycortisol, for which there is no known physiological function (Weiss & Richards 1970). This is further complicated by possible effects due to high affinity corticosteroid binding proteins and interactions with other steroid hormones (Sernia, Bradley & McDonald 1979; McDonald, Martin & Than 1981). McDonald *et al.* (1981) found no evidence for a sex difference in adrenal function. Booth *et al.* (1988) and McDonald *et al.* (1988) found that although there was no consistent pattern of changes in peripheral cortisol concentrations or metabolic clearance with stress or disease, chlamydially infected Koalas have related hormone metabolism parameters (larger volume of ingestion and larger half-life of cortisol and testosterone) which vary from apparently healthy animals (McFarlane & Carrick 1988).

Apart from the finding by Yesberg, Butz-Olsen & Sharples (1967) of antidiuretic activity, very little is known of structure/function relationships of either the adenohypophysis or the neurohypophysis of the Koala.

Descriptions of the thymus of this species were reviewed by Yadav (1973). Both superficial cervical and thoracic lobes may be present, although usually the thoracic lobes are absent or very small. This is the reverse of the usual situation in eutherians and most marsupials, where only the thoracic component is present and in the phalangeroids where both components are well represented. It is a trait shared, however, with the vombatids (where the thoracic component does not develop).

The thyroid consists of two lobes about 25 mm long, 5 mm wide and 3 mm deep. Typically, it lies between the fourth and ninth tracheal rings and it lacks an isthmus. The right lobe tends to exhibit more variability in size and location than the left and accessory thyroid tissue may be present. Blood supply is from the common carotid artery and venous return via the internal jugular vein (Martin 1836; Owen 1868; MacKenzie & Owen 1919b; Sonntag 1921a).

Descriptions of the pancreas in this species indicate that, at least superficially, it is typically mammalian (Martin 1836; MacKenzie 1918b; Sonntag 1921a). An unusual feature in the Koala, however, is the presence of a 20 mm long, thin-walled, saccular dilation of the pancreatic duct prior to its entry into the duodenum in close proximity to the common bile duct (MacKenzie 1918b). Kratzing (1981) believes the animal can store and concentrate pancreatic secretion and deliver it to the duodenum in a manner analogous to the delivery of bile from the gall bladder. Nothing is known of the endocrine function of this compound gland.

The gross and microscopic structure of the sternal gland present in male Koalas has been described by MacKenzie & Owen (1919b) and Degabriele (1981a). It can be up to about 85 mm long x 50 mm wide and contains both sudoriferous and sebaceous components of a generally similar nature to that found in equivalent glands in other marsupials. It lacks underfur on its surface. The gland undergoes conspicuous seasonal changes in activity, presumably under androgenic control and is used for scent-marking of trees (Smith 1980b). A range of fatty acid derivatives, monoterpenes and sesquiterpenes has been identified as secretory products, but none appears suitable for use as a pheromone by the species. Some of these compounds are possibly contaminants from the eucalypt leaf diet, rather than endogenous to the Koala (Carman & Greenfield 1981).

Reproduction

The diploid chromosome number of the Koala is 16 with an XY/XX sex determination mechanism (Greenwood 1923).

The female reproductive tract exhibits a number of minor differences from the usual marsupial arrangement which, in aggregate, produce a distinctive morphology (Fig. 31.5). The ovaries tend to be flattened and their enveloping fimbria are located within small peritoneal diverticula. The Fallopian tubes are not very convoluted and there is a relatively slight and gradual change in diameter as they join the duplex uteri. The uterine cervixes are well developed and the tough cervical tissue can be easily palpated through the wall of the vaginae. Vaginal caeca are absent and even bulging of the cranial end of the vaginal complex does not occur. The vaginal culs-de-sac descend directly towards the urogenital sinus, normally remain divided by a median septum and do not form a permanent, patent connection to the sinus. Fairly typical lateral vaginae are bound by connective tissue to the 'median vagina' thus formed. On each side, the cranial portion of the vaginal cul de sac receives the uterine cervix. On the lateral wall of each median vaginal canal the corresponding lateral vagina enters about 5 mm caudal to the cervix. The bilobed clitoris is

relatively prominent (about 5 mm long) located on the ventral surface of the outlet of the urogenital canal (Forbes 1881; MacKenzie 1919; Brown *et al.* 1984a).

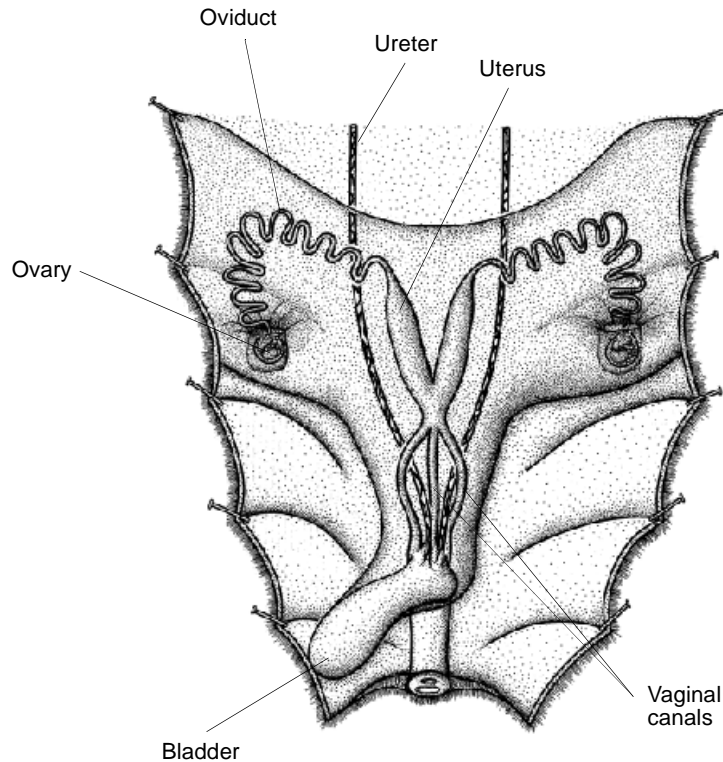


Figure 31.5 Reproductive tract of a female *Phascolarctos*. Scale $\times 0.23$.
(© ABRS) [S. Collin]

The widespread infertility prevalent in the Koala may be directly related to the distinctive anatomical arrangement of the female reproductive tract (Backhouse & Bolliger 1961; Finckh & Bolliger 1963; MacKenzie 1919). The aetiological agent responsible for the lesions of the reproductive tract causing the infertility condition is the bacterium, *Chlamydia psittaci*, although other predisposing factors are most likely involved (Brown *et al.* 1984a; McColl *et al.* 1984).

The female is seasonally polyoestrous. The average cycle length is 35 days (Handasyde 1986), similar to the reported gestation period of 34–36 days (Smith 1979b; Brown, Carrick & Gordon 1981a). At most, females normally give birth to one young per year, though Eberhard (1972) recorded a single set of twins.

There is no evidence that embryonic diapause occurs in this species. It has been suggested that the breeding season commences earlier in the northern part of the species' range, but this was discounted by Martin & Lee (1984). They observed that births occur between August and May on French Island, Victoria, with 80% of births confined to the period between the beginning of November and the end of March. Oestradiol and progesterone occur in relatively small amounts in peripheral plasma of this species, rising during the breeding season (Handasyde 1986). In females, testosterone is present at about 10% of the mean concentration in males. Detailed endocrine profiles during the reproductive cycle are not available (Brown, Carrick & Gordon 1981b).

The male reproductive tract is of fairly typical marsupial form, with a relatively small cordate prostate, three pairs of Cowper's glands and a distinctly bifid penis (Young 1879). MacKenzie (1919) also described the male tract of this species, but misidentified two pairs of Cowper's glands as 'ductless sex glands'.

In a landmark paper, Hughes (1965) showed that at the light microscope level the heads of mature sperm of Koalas and Wombats species share features which make them unique amongst marsupials. During spermiogenesis, the nuclear chromatin condenses in an uneven manner reminiscent of the pattern in the Platypus, *Ornithorhynchus anatinus* (Harding, Carrick & Shorey 1981a; Carrick & Hughes 1982; Fig. 31.6). The mode of nuclear flattening, relative to the flagellum, differs from that in other marsupials and this results in the unusual 'eutherian-like' neck insertion of sperm of this species. These features are taken as indications of a primitive condition rather than as evidence of convergence.



Figure 31.6 Longitudinal section through an epididymal spermatozoon of a *Phascolarctos*. Magnification $\times 12,600$. A = acrosome; an = annulus; MP = midpiece; mt = mitochondrial helix of midpiece; N = nucleus; pp = principle piece; ep = end piece. Also shown are transverse sections of other spermatozoa.

Another extraordinary feature of the testis of the Koala is the presence of crystalloid inclusions in the basal region of Sertoli cells, which resemble the Charcot-Bottcher crystalloids of human Sertoli cells (Harding, Carrick & Shorey 1981b).

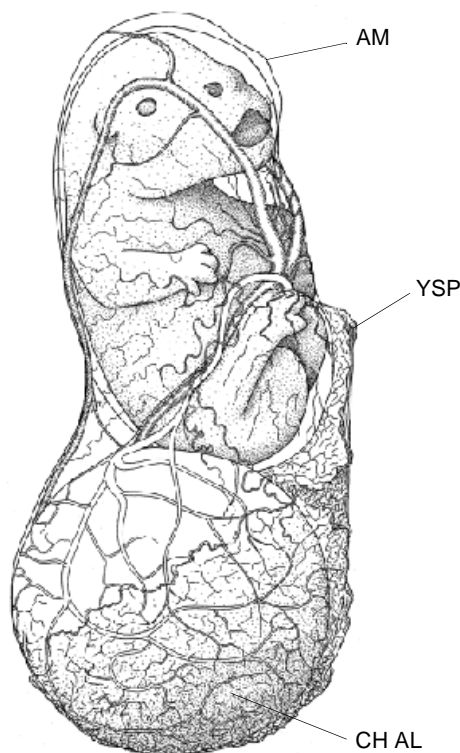
In a study of 24 hour androgen secretion profiles in the Koala, Carrick *et al.* (1981) reported the first unequivocal evidence for episodic release of androgens in a male marsupial. In the breeding season, mean testosterone concentrations of about 1 ng/ml commonly rise to about 5 ng/ml of blood. In the non-breeding season, rather less is detected (mean 0.5 ng/ml blood). Androstenedione concentrations do not vary much between the breeding and non-breeding seasons (mean 1.5 ng/ml blood; peak 4 ng/ml). More oestradiol is usually found in males than is typical of females.

Male Koalas mate with any receptive female without elaborate courtship. Coitus usually takes place in a tree, the male mounting from behind whilst grasping the female by the nape of the neck with his teeth. A plug of coagulated semen may occlude the urogenital canal of the female following copulation (Smith 1979b). Typically, both sexes appear to reach sexual maturity at 2 years of age (Martin & Lee 1984), although, as discussed later, the age at which the first mating occurs may vary.

Embryology and Development

The Koala is one of the few marsupials to develop a chorioallantoic placenta, usually considered the hallmark of the Eutheria (Fig. 31.7). The allantois has an extensive area of fusion with the chorion, but no chorionic villi form and there is no fusion with the endometrium in this region nor over the surface of the vascularised trilaminar yolk sac. Implantation occurs, however, in an annular zone of the non-vascular bilaminar yolk sac, just outside the sinus terminalis (Caldwell 1887; Pearson 1949; Hughes 1974, 1984).

Figure 31.7 A full-term Koala foetus (17 mm long) with partially removed foetal membranes. Most of the outer covering of yolk sac placenta has been dissected away to reveal the amnion (AM), closely investing the fetus and the chorioallantoic placenta (CH AL). But parts of the yolk sac membranes still adhere (YSP). Scale x 3.2. (After R.L. Hughes, personal communication; © ABRS) [G. Scott]



If Hill (1949) was correct in considering the simple apposed chorioallantoic-omphalopleural placenta as seen in Koalas and wombats as the most primitive type among the Marsupialia, it could be taken as further evidence of the separate stem group nature of the Phascolarctidae, a notion which also found some support from the studies of sperm fine structure alluded to above (Harding *et al.* 1981a).

Following birth, the offspring spend the first 6 months of life in the pouch feeding on milk (Eberhard 1978; Martin & Lee 1984). When the pouch young first starts to poke its head out of the pouch at about 5 months of age, it is fed on 'pap', a soft green fluid produced by the female only about this time and considered to be the evacuated contents of the caecum. This material has been suggested to form an innoculum for the young's caecum, which seems likely since this phenomenon coincides with the commencement of a phase of exponential growth, eruption of the first teeth and the ingestion of leaves (Minchin 1937; Martin & Lee 1984).

The young stays in close association with its mother after it vacates the pouch until at least 11 months of age, at which time it is about half grown. Depending on season and locality, it may then either disperse or continue to associate with its mother for up to another year. Juvenile males usually disperse before females (Gordon, McGreevy & Lawrie 1981; Martin & Lee 1984).

NATURAL HISTORY

Life History

The age at which females produce their first young varies. In Victorian populations, about 10% produce their first young in their second year and 80% their first young in their third year (Martin & Lee 1984). Although males appear sexually mature at 2 years of age, most males may not get an opportunity to mate until their growth asymptotes in their fourth year, or even later. Although young males attempt to mate, they are prevented from doing so by older, larger males in their vicinity (Martin & Lee 1984). Females tend to produce one young a year in populations where fertility is not impaired by chlamydiosis.

In the Victorian populations studied by Martin (1981), reproductive rates are as high as 80–84% in *Chlamydia*-free females up to 10 years old, but then decline to 40–60%. The variability in reproductive rates between populations is considerable; only 10–15% of *Chlamydia*-infected females produced young on Phillip Island, Victoria, between 1977 and 1981 (Martin 1981; Martin & Lee 1984). Low reproductive rates have thus been attributed to lowered fertility due to chlamydiosis (Brown *et al.* 1984a; McColl *et al.* 1984) and poor nutrition associated with defoliation of food trees (Martin 1981; 1985b). Maximum longevity of females in the wild is in the order of 15 years, but is probably less for males (Martin & Lee 1984). Martin (1983) found few males with worn teeth in Victorian populations and suggested that old males died after being forced from the reproductive population. By contrast, females with worn teeth were not uncommon.

Ecology

The Koala is primarily an animal of open forests and woodlands in which trees of the genus *Eucalyptus* predominate. It feeds almost exclusively upon the foliage of a range of *Eucalyptus* species (Pratt 1937; Eberhard 1978; Hindell *et al.* 1985). Usually one or two species are favoured in communities comprising a mixture of *Eucalyptus* species. In southern Australia, up to 24 species of *Eucalyptus* are known to be eaten by Koalas, but the Manna Gum, *Eucalyptus viminalis*, and the Swamp Gum, *E. ovata*, are commonly the preferred species

(Eberhard 1978; Warneke 1978; Hindell *et al.* 1985; Martin 1985a), whereas in New South Wales and Queensland the favoured species are the Grey Gum, *E. punctata*, and the Forest Grey Gum, *E. tereticornis* (Eberhard 1978). Nevertheless, Koalas are occasionally found feeding on foliage of other genera (*Acacia costata*: Robbins & Russell 1978; Black Wattle, *A. mearnsii* and Blackwood, *A. melanoxylon*: Hindell *et al.* 1985; Northern Cotton Tree, *Bombax ceiba*: Degabriele 1973; and *Lophostemon confertus* and *L. saueolens*: Pearse & Eberhard 1978). Lithgow (1982) reported Koalas living in and feeding on the exotic *Pinus radiata*. There also is evidence that preference for *Eucalyptus* species changes with season (Williams 1971; George 1977; Eberhard 1978; Hindell *et al.* 1985), that different individuals have different preferences and that some trees of a species are favoured more than others (Hindell *et al.* 1985). There is presently no satisfactory explanation for the dietary preferences of the Koala. It has been proposed that the animals avoid the foliage of some eucalypts because of the allochemical content and select others because of their essential oil content. These hypotheses were reviewed and dismissed by Eberhard (1978) and Southwell (1978).

Degabriele (1981b; 1983) suggested that the abundance of the Koala is limited by the amount of nitrogen available to them in their food, basing this hypothesis on the observation that nitrogenous compounds are relatively scarce in the diets of herbivorous animals (White 1978). Although Ullrey, Robinson & Whetter (1981) observed that the concentrations of crude protein are significantly higher in browse that Koalas prefer in captivity and in the young leaves that they prefer when given the choice, Hindell (1979) was unable to establish a relationship between the protein content of foliage and species preference in a natural population.

On Kangaroo Island, South Australia, adult Koalas are generally sedentary, using about 15 trees within a home range of 1–2.5 ha (Eberhard 1978). Adjacent trees are often used with very different frequencies. Home ranges are largely exclusive, although the home ranges of some males spatially overlap those of females and they share some trees. Juveniles disperse from the maternal range between 18 months and 2 years of age and may continue to wander until 4–5 years of age (Eberhard 1978).

The Koala has been described as non-verminous (Eberhard 1978) and indeed, seems to harbour few parasites. The cestode *Bertiella obesa* has been found in the small intestine (Mackerras 1958). Roberts (1970) found that Koalas harboured five species of ticks: *Ixodes holocyclus*, *I. tasmani*, *I. hirsti*, *I. cornuatus* and *Haemaphysalis bancrofti*. *Ixodes holocyclus* may cause paralysis in the Koala, but Dickens (1978a) suggested that the species seems to have general resistance.

Evidence for diseases thought to afflict Koalas was reviewed by Dickens (1978b). Among the diseases that appear to be demographically significant in natural populations are: anaemia, which could be attributed to nutritional deficiencies; massive tick infections by an organism similar to *Haemobartonella*; or malignant blood disease; pneumonia which has been identified as a significant cause of mortality of Koalas in Queensland; and a group of diseases that have been associated with the bacterium *Chlamydia psittaci* (Cockram & Jackson 1976; Brown *et al.* 1984a; Brown, Carrick & Gordon 1984b; McColl *et al.* 1984). Martin (1985b) attributed loss of condition, mortality and infertility in a population of Koalas at Walkerville, Victoria, to a microcytic anaemia associated with massive tick infestations and trace element deficiency. Infertility elsewhere has been attributed to an ascending infection of the reproductive tract (Obendorf 1981) associated with infections of *Chlamydia psittaci* (McColl *et al.* 1984; Brown *et al.* 1984b). Two other diseases which cause debilitation, dirty tail and kerato-conjunctivitis have also been associated with infections of *C. psittaci* (Cockram & Jackson 1976; Brown *et al.* 1984a). It

seems likely that chlamydiosis was responsible for most of the disease epizootics cited by Troughton (1967) as the cause of declines in Koala populations between 1887-89 and 1900-03.

Historically, the principal predators of Koalas appear to have been Aborigines, who regarded them highly as food, and the dingo, which caught individuals when they came to the ground to move between trees (Parris 1948; Warneke 1978; Strahan & Martin 1982). Today, the only known predators are the Wedge-tailed Eagle, *Aquila audax*, and the Powerful Owl, *Ninox strenua*, both of which are known to take juveniles (Eberhard 1978).

Behaviour

Koalas are principally arboreal and only come to the ground to move between trees. They spend most of the day resting in trees and are most active in the late afternoon and at night. Feeding occurs at all times of the diel cycle, but predominantly in the early evening. Hindell *et al.* (1985) found that the total time spent feeding ranged from 1.8–3.8 hours per day.

Most of the descriptions of the behaviour in the Koala come from observation of animals in captivity by Smith (1979a, 1979c; 1980a, 1980b, 1980c). The principal social interactions observed were between mother and young and between adults during the breeding season. Cubs which have recently emerged from the pouch ride on the belly of the female, but later ride on the back with the belly pressed against the mother. Small cubs return to the pouch to suckle, but older cubs suckle from outside of the pouch. Suckling ceases by the 13th month. Cubs first show independence from the mother at about 11 months of age when they are observed to sit apart from the mother. The association ends when the young is about 18–24 months of age (Smith 1979c).

Copulation is not preceded by courtship and is often attempted by males during the breeding season. Most attempts are unsuccessful. Although the male may successfully mount the female, she does not respond with curvature of the back. Females often attempt to fight off males. Successful copulations last only one or two minutes; the male climbs over the back of the female and grips the back of her neck with his incisors while both hold onto a branch or trunk. The head of the female is stretched back and the lumbar region of the male is thrust forward so that he gains intromission from behind. After a short bout of thrusting, both the male and female show contractions of the abdomen. Disengagement often is forced by the female (Smith 1980c).

Adult males mark the base of trees they are climbing with the secretion from the prominent sternal gland. During this procedure, the chest is flattened against the trunk and rubbed up and down about six times (Smith 1980b). This behaviour is first observed in males 3 years of age, but increases in frequency with age and peaks when males are 5 years old. Smith (1980b) did not observe any consistent response to marked objects.

Koalas emit a number of sounds of which the most frequent are a bellow, principally emitted by the male and a cry and wail which females emit when approached by males (Smith 1980a). Males often bellow spontaneously and most frequently during the mating period. Sometimes, males appear to bellow in response to the bellows of other males and following encounters.

Economic Significance

In the second half of the last century and the first decades of this century, substantial numbers of Koalas were killed for pelts. One million pelts were sold as a result of a 6 month open season in Queensland in 1919 and 584 738 pelts were sold from the last open season, lasting one month, in 1927 (Gordon & McGreevy 1978). Today, the animal is an important tourist attraction.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Koala is found in eastern and south-eastern Australia from about Atherton, Queensland to Wilson's Promontory, Victoria (Fig. 31.8). It is most common on the coastal plains and tablelands of the Great Dividing Range, but also occurs on the inland slopes and plains (at least as far west as Charleville, Queensland), especially along rivers (Gall 1978; Gordon & McGreevy 1978; Warneke 1978).

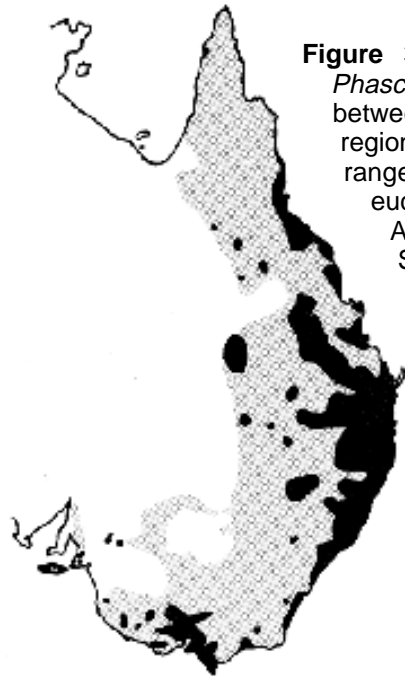


Figure 31.8 Historic and present distribution of *Phascolarctos*. Reliable sightings of animals between 1960 and 1981 are shown in black. These regions represent the probable historic maximum range of the species. The approximate limit of eucalypt forest and woodland in eastern Australia is depicted by stippling. (After Strahan & Martin 1982)

The distribution of the Koala at the time of European settlement cannot be precisely defined as it was infrequently referred to in early historical records. All of the records in Victoria prior to 1850 were from the densely forested eastern sector of the State (Warneke 1978). Yet in the next 50 years, it became extremely abundant in many areas of open forest for which there were no early records, such as the *Eucalyptus camaldulensis* forests along the rivers north of the Great Divide (Parris 1948). This rise in abundance has been attributed to the decline in hunting by Aborigines and predation from dingoes (Parris 1948; Warneke 1978; Strahan & Martin 1982). During the early decades of this century dramatic decline in numbers occurred as a consequence of hunting and outbreaks of disease (Troughton 1967), mortality associated with bushfires and clearing of habitat (Strahan & Martin 1982). By the 1930s, the range of the species was substantially reduced to small and often isolated populations (Gordon & McGreevy 1978; Warneke 1978). Koalas were formerly common in south-eastern South Australia (Jones 1923a), but by the late 1930s was considered extinct in that State (Robinson 1978). It was introduced into Flinders Chase National Park from Victoria through releases in 1923 and 1925. Individuals from this Park have been released subsequently at sites along the Murray River, southern Eyre Peninsula, Mount Lofty Ranges and in the southeast near Lucindale (Robinson 1978). Koalas, taken principally from Victoria, have been introduced into Tidbinbilla Nature Reserve, Australian Capital Territory, on a number of occasions since 1939 (Braysher 1978). In Victoria, individuals have been translocated from island populations where they were damaging trees to

many localities within the former range of the species, so that the status of the species now appears secure (Strahan & Martin 1982). In Queensland, the range of the species may still be declining (Gordon & McGreevy 1978).

Affinities with other Groups

The relationships of the Phascolarctidae to other marsupials have been a matter of contention. Broadly, there have been two opposing views. The suggested relationship with the pseudocheirids is based upon their common possession of selenodont molars and forcipate hands (Bensley 1903; Jones 1923a). The other, now accepted, view is that the phascolarctids are related to the vombatids. Sonntag (1921a) reached the latter view after a comprehensive study of their morphology, and has received support from an analysis of sperm morphology (Hughes 1965) and serology (Kirsch 1968, 1977a). These relationships were reviewed by Strahan (1978) and Archer (1978c, 1984d), who both supported Sonntag's contention and suggested that the forcipate hand in the Koala has been developed independently (Strahan 1978) and that selenodonty is a synapomorphic condition in all diprotodonts (Archer 1978c).

Affinities within the Phascolarctidae

Archer (1978c, 1984d) provided a cladistic analysis of the relationships of the Koala and the five extinct taxa currently recognised within the Phascolarctidae. This analysis, based largely upon dental characters, suggested that these taxa fall into three lineages: a lineage represented by *Litokoala* which is characterised by structurally plesiomorphic characters, such as the retention of a well-developed metaconule on the upper molars; a lineage represented by *Perikoala* and *Phascolarctos* (both species), which share a number of derived characters including extremely complex wrinkling of the crowns of the molars and buttress crests on the posterolingual face of the paracones; and a lineage represented by *Koobor*. *Perikoala* and *Phascolarctos* share a number of derived characters with *Koobor* (both species), such as a reduced metaconule and reduced lingual buttresses on the metacone of M1, but *Koobor* is distinctive in retaining the fewest plesiomorphic characters and is characterised by derived characters such as a marked bicuspid condition of P4, closed buccal basins on the paracones, markedly narrow upper molars and buccally displaced protocones and hypocones. As Archer (1984d) acknowledged, the unusual feature of this analysis is that *Litokoala* is the most plesiomorphic of these phascolarctids, despite being younger than *Perikoala*, and the same is true of *Phascolarctos* and *Koobor*.

Fossil Record

Archer (1984d) recognised five extinct taxa in his review of the fossil phascolarctids. *Perikoala palankarinnica* is known from an almost complete upper and lower dentition, a skull and postcranial fragments from the Middle Miocene Ngapakaldi fauna of South Australia. *Litokoala kutjampensis* is represented by a single upper molar from the Late Miocene Kutjampu fauna, and also from north-eastern South Australia. The genus *Koobor* includes two species, *Koobor notabilis*, represented by five upper teeth from the Pliocene Chinchilla fauna from south-eastern Queensland, and *K. jimbarrati*, represented by an upper molar from the Pliocene Allingham fauna from northeastern Queensland. *Phascolarctos*, which contains the only extant phascolarctid, also includes *Phascolarctos stirtoni*, known from three upper teeth from a Pleistocene deposit at Gore, south-eastern Queensland. *Phascolarctos stirtoni* appears to have been larger than the extant species, a trend found among some other Pleistocene-Recent species pairs (Archer 1984d).

Maintenance

Koalas are maintained in captivity for public display and scientific research in several zoos and sanctuaries in Australia and in zoos overseas. Many captive colonies are breeding successfully. Exportation of animals is monitored by the Australian National Parks and Wildlife Service through the Wildlife Protection (Regulation of Exports and Imports) Act 1982.

The design of enclosures, supply of food and other aspects of the husbandry of Koalas were detailed by Drake (1978). Sufficient shelter from wind, rain and extreme heat and adequate space for movement are important considerations in the design of enclosures. A year-round supply of fresh leaves of favoured species of *Eucalyptus* is required to maintain animals in good health. Recent work on the development and refinement of a 'eucalypt biscuit' comprised predominantly of eucalypt leaves indicates that the nutritional requirements of Koalas could be sustained, at least over short periods of time, when fresh food is lacking (I.D. Hume, personal communication).

Captive Koalas require behavioural and clinical observation. Animals are susceptible to a variety of diseases, particularly conjunctivitis and urinary tract infections and stress. Treatment of seriously ill animals is subject to failure as they do not eat and frequently die of starvation (Drake 1978). A similar problem is experienced when traumatised or diseased animals are brought into captivity from the wild for treatment (Blackshaw *et al.* 1988).

Orphaned Koalas have been successfully raised using a variety of food supplements. Currently, a 50:50 mixture of Portagen and Farex is recommended. This is best administered using a small feeding bottle with a large hole (2-3 mm diameter) in the teat (Brown & Sargent 1988).

CLASSIFICATION

Three subspecies of the Koala, *Phascolarctos cinereus*, have been described. Thomas (1923) established *P. c. adjutus* for populations at the northern extent of the range, whereas Troughton (1935) referred Victorian populations to *P. c. victor*, leaving the populations in New South Wales as the nominate subspecies. These subspecies were distinguished on adult size, pelage thickness and colour, but probably represent part of a north-south cline.

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