FAUNA *of* AUSTRALIA

29. MACROPODIDAE

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Red Kangaroo–*Macropus rufus* [Australian Photo Library]

Rufous Hare Wallaby–*Lagorchestes hirsutus* [F. Knight/ANPWS]

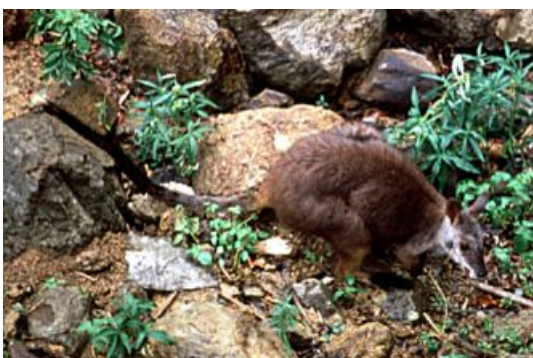Red Kangaroo–*Macropus rufus* [CSIRO Wildlife & Ecology]

Suckling Tammar Wallaby attached to the teat; the larger teat provides milk to a young-at-foot–*Macropus eugenii* [CSIRO Wildlife & Ecology]

Antilopine Walleroo–*Macropus antilopinus* [CSIRO Wildlife & Ecology]

Bridled Nailtail Wallaby–*Onychogalea fraenata* [M. Evans]

Proserpine Rock Wallaby–*Petrogale persephone* [B. Nolan]

Nail of Bridled Nailtail Wallaby–*Onychogalea fraenata* [M. Evans]

Banded Hare-wallaby–*Lagostrophus fasciatus* [CSIRO Wildlife & Ecology]

Quokka–*Setonix brachyurus* [Australian Photo Library]

DEFINITION AND GENERAL DESCRIPTION

The family Macropodidae comprised 40 extant species at the time of white settlement (Calaby & Richardson 1988) and included the kangaroos, wallaroos, wallabies, hare-wallabies, nail-tail wallabies, rock-wallabies, pademelons, quokka, tree-kangaroos and swamp wallaby. The family is combined with the Potoroidae in the Macropodoidea. Macropodids range in size from the small hare-wallabies, weighing about 1 kg, to the Red Kangaroo, *Macropus rufus*, and Eastern and Western Grey Kangaroos, (*M. giganteus* and *M. fuliginosus* respectively), in which males may stand more than 2 m tall when erect and weigh more than 80 kg. The teeth and feet of macropodid marsupials clearly place them within the suborder Diprotodonta, but as suggested by their family name, macropodids have larger hind feet and more powerful hind limbs which provide a characteristic fast hopping gait. In all extant macropodids the fourth digit of the hind foot is enlarged and, with the smaller fifth digit, forms the main weight- bearing structure of the foot. The first digit is absent and the second and third digits are very small and syndactylous, as in all other diprotodont marsupials. The tail is large and provides balance during bipedal locomotion or stabilisation during slower quadrupedal movements, for example, during feeding or fighting. Most macropodids have either 32 or 34 teeth with the following dental formula: I 3/1 C (1)/0 PM 2/2 M 4/4 (Kirkpatrick 1978).

Dentition is typically diprotodont with a large single pair of forward-projecting lower incisors and a large diastema between these and the first premolars. The small, degenerate lower incisors seen in phalangerid species are absent. The mandibular masseteric fossa forms a deep cavity which extends beneath the molars. Molar eruption and progression occur during life and the changing tooth patterns within species are distinctive enough to indicate various age classes within populations.

Macropodids possess hairy, robust, non-prehensile tails, large well-developed ears, moderate equisized claws on the forepaws, minute or absent canines, transversely ridged molars which increase in size posteriorly and a patent median vaginal canal. In the larger macropodids, adult males are considerably larger than females and in the Red Kangaroo and the Common Wallaroo, *Macropus robustus*, there is also a sexual dimorphism in adult pelage colour. The pouch of all macropodids is well formed and opens anteriorly with four teats, each associated with one of four mammary glands. A single young is produced after about 1 month gestation and in most a second young, conceived following a post-partum oestrus, is held in embryonic diapause during lactation.

Most macropodids are nocturnal, although some of the larger species are active in early morning and late afternoon. All are grazing and/or browsing herbivores with large, sacculated stomachs adapted for a ruminant-like digestion of plant materials. Habitats into which macropodid species have evolved cover a broad spectrum from arid central plains and ranges to dense temperate and tropical coastal forests. They are found in a wide range of terrestrial environments in Australia, New Guinea and some adjacent islands. Sustaining feral populations also now exist in New Zealand, Hawaii, Scotland, Germany and England, following intentional introductions or zoo escapes.

HISTORY OF DISCOVERY

The earliest European reference to a macropodid marsupial was made in 1629 by the Fleet Commander of the Dutch East India Company, Francisco Pelsaert, aboard the ill-fated *Batavia*, which was wrecked on the southern edge of Morning Reef off the Abrolhos Islands in the Houtman Archipelago, 37 nautical

miles from the western coast of Australia (Frith & Calaby 1969). The marsupial Pelsaert so accurately described in his journals was the Tammar Wallaby, *Macropus eugenii*, which today still abounds on the off-shore islands of our southern and western coastline. Shortly after, Volckersen, in 1658, and de Vlamingh, in 1696, landed on Rottnest Island off Perth and were the first to describe the Quokka, *Setonix brachyurus*. De Vlamingh named Rottnest in reference to the abundant 'rats'. Another island dweller, the Banded Hare-wallaby, *Lagostrophus fasciatus*, was the next macropodid to be described after William Dampier in 1699 landed on Dirk Hartog Island off the coast near Carnarvon.

These three small macropodids were all discovered in the west. Subsequent descriptions of eastern members of the kangaroo family had to await Cook's journey to Australia. The first mention was in his journal entry of 23 June, 1770, whilst at the place which would become Cooktown on the Endeavour River. This animal was probably the Common Wallaroo (Frith & Calaby 1969). The first picture published of a member of the Macropodidae (the New Guinean Brown Pademelon, *Thylogale brunii*) was a plate in de Bruin's book of travels in 1714. Kangaroos were not recognised as members of a distinct group until Shaw coined the generic name *Macropus* in 1790. Surprisingly, captive kangaroos were breeding in England by 1794 (Frith & Calaby 1969).

Several French expeditions contributed type specimens of macropodids: Baudin (1800– 1804 expedition) - several wallabies and the Western Grey Kangaroo; Freycinet (1819 expedition) - the Red Kangaroo.

Most taxonomic activity in the 19th Century was due to John Gould and his collectors, notably John Gilbert. In 1838–1840 Gould worked in Tasmania, South Australia and New South Wales. Gilbert collected in 1839–1845 in Western Australia, New South Wales and Queensland, a career cut short when he was killed by Aborigines in 1845 while a member of Leichhardt's first expedition. Gould was responsible for describing around one-third of the recognised species of the Macropodidae.

The two Australian tree kangaroos, Lumholtz's Tree-kangaroo, *Dendrolagus lumholtzi*, and Bennett's Tree-kangaroo, *D. bennettianus*, were described from Queensland rainforests by Collett (1884) and De Vis (1887).

The Parma Wallaby, *Macropus parma*, was considered extinct in 1932, but was discovered in 1965 in New Zealand where it had been introduced to Kawau Island in the 1880s. It was rediscovered subsequently near Gosford in 1967 and in several other coastal and tableland areas of New South Wales (Maynes 1974).

Most macropodid type specimens (at least 27) are lodged in the British Museum and seven are present in the Paris Museum. Many of the early type specimens collected by Dutch, French and English explorers, however, were lost or destroyed, for example, those of the Eastern Grey Kangaroo, the Black-striped Wallaby, *M. dorsalis*; the Tammar Wallaby; the Western Brush Wallaby, *M. irma*; the Red-necked Wallaby, *M. rufogriseus*; the New Guinean Brown Pademelon; the Brush-tailed Rock-wallaby, *Petrogale penicillata*; and the Unadorned Rock-wallaby, *P. inornata* (Thomas 1888). Two (New Guinean) type specimens from the genus *Dendrolagus* were originally sent to the Leyden Museum (the White-throated Tree-kangaroo, *D. ursinus*, and the Grizzled Tree-Kangaroo, *D. inustus*). The (New Guinean) types of the Macleay's Dorcopsis, *Dorcopsulus macleayi* and Doria's Tree-kangaroo, *Dendrolagus dorianus* were lodged with the Macleay Museum, Sydney.

Today, there are about 52 recognised species of recent macropodids in Australia and New Guinea and, of these, at least five are extinct or presumed to be, including the Toolache Wallaby, *Macropus greyi*. This, 'the most beautiful and

elegant of wallabies' (Jones 1924), was hunted to extinction and has the dubious honour of being the largest macropodid to have become extinct since European colonisation. Four other species are considered endangered (Archer *et al*. 1985).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The general body form of macropodids is dominated by adaptation to their distinctive high-speed locomotion: hopping or bounding with the forefeet clear of the ground (Fig. 29.1). Thus, the hind limbs are much longer and more heavily muscled than the forelimbs. The region of the pelvic girdle (hips, lower back, and thighs) is far bulkier than that of the pectoral girdle (shoulders, upper chest and upper arms). The animal's centre of mass lies in the pelvic area. This contrasts with large, terrestrial eutherian herbivores, such as the Bovidae, Cervidae, Suidae and other ungulates, or with wombats, in which the thoracic and abdominal trunk of the animal is cylindrical and supported at each end by limbs of equal length. The major role in propulsion and mass-suspension is given to the hind limb girdle. The body anterior to the lumbar region is freed and highly mobile (Fig. 29.1d). Macropodids, while supported squarely on the plantigrade hind feet, can crouch to feed, sit up to reach higher plants or, when alert, twist around to groom the back or tail, stand up to fight, or hop slowly or quickly. The animal may get additional support from the tail, giving it a stable 'tripod' base. This flexibility allows macropodids to feed on plants from ground level to head height without the ungulate's need for a long neck. Macropodid neck length is equal to or less than head length.

The head is similar in proportions to that of small and medium bovids and cervids (Fig. 29.2). The eyes are about midway along the head, the muzzle about as long as the postorbital cranium. The eyes are of medium size, widely set and orientated to give wide lateral monocular and some forward binocular vision. The external ears are set back, are high and the pinnae are mobile, especially
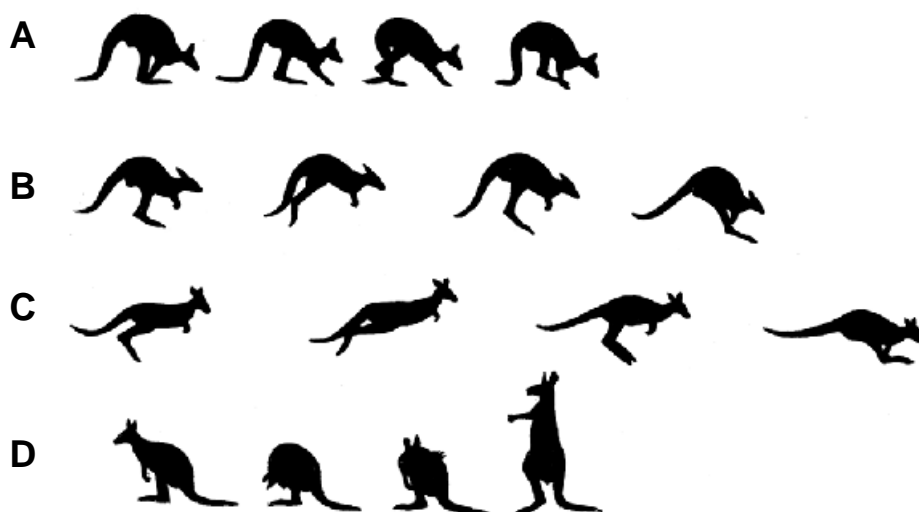

Figure 29.1 Silhouettes of red kangaroos to show: **A**, slow pentapedal locomotion; **B**, low-speed bipedal hopping (15-35 km per hour); **C**, high-speed hopping (40-50 km per hour); **D**, the mobility of the anterior part of the body relative to the pelvis (A, B & C after Dawson 1977; © ABRS).

[B. Scott & F. Knight]

capable of rotation. The muzzle tapers to a generally narrow and not very deep nasal region. The nares are slit-like, set in a V above a divided upper lip and surrounded by a relatively narrow, bare rhinarium. There are rows of whiskers above the upper lips. The lower jaw is shallow and, because of the diprotodont lower incisors, much shallower distally than the mandible of an ungulate of similar size. The angle of the mandible is quite deep and square and the jaw at this point is slightly narrower than the cheek bones.
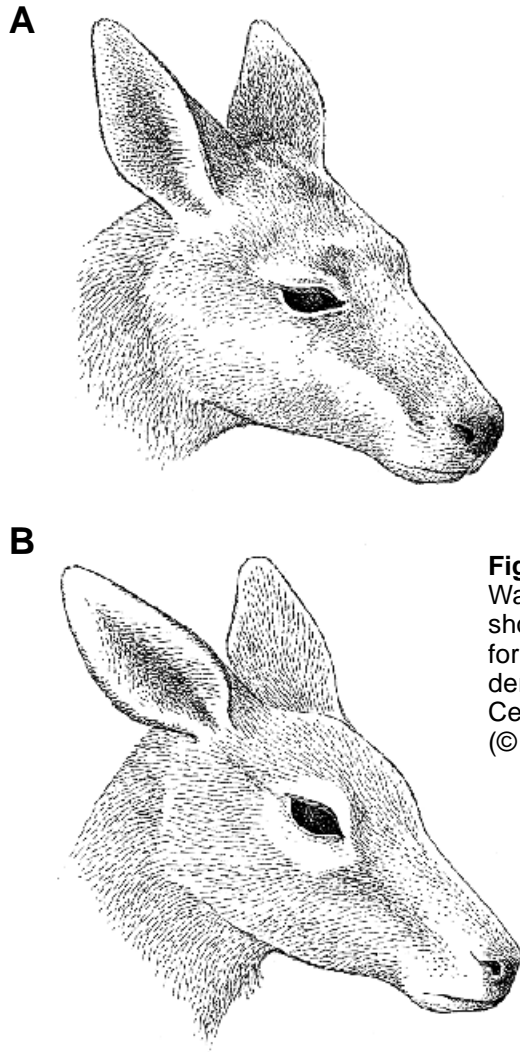
A

B

Figure 29.2 A, Head of the Antilopine Wallaroo and **B**, *Odocoileus hemionus* showing the adaptive convergence in form seen in these two independently derived groups (Macropodidae and Cervidae) of large herbivores. (© ABRS)   [F. Knight]

Macropodids do not possess any cranial or dental weapons: no horns, antlers, cranial knobs, tusks or enlarged canines. The articulation of the head with the neck is very flexible, enabling the muzzle to remain horizontal whether the neck is horizontal or vertical. The shoulders are narrow and the thorax flares from a markedly narrow upper rib-cage to the large abdomen. When the animal is crouched, the bulk of the abdomen hangs between the hind legs.

The cloaca opens at the end of a large protuberance on the lower surface of the abdomen just in front of the junction with the tail. Anterior to the cloaca on the belly is either the scrotum (as in all marsupials, descended testes lie anterior to the penis, not posteriorly, as in most Eutheria) or the pouch. The pouch opens forward at about the level of the hips and is very deeply invaginated. When occupied by a large juvenile it stretches greatly, occupying most of the posterior abdominal surface and almost touching the ground. The opening is broad when relaxed. When unoccupied, it contracts and the opening is held closed. The pouch contains four nipples.

The penis can be protruded from the cloaca. Bifurcate adornments found in many other metatherian families are absent. It is strongly reflexed anteriorly when erect. In most macropodids the penis has a long, distally tapering, conical glans (Rodger 1978; Rodger & Hughes 1973).
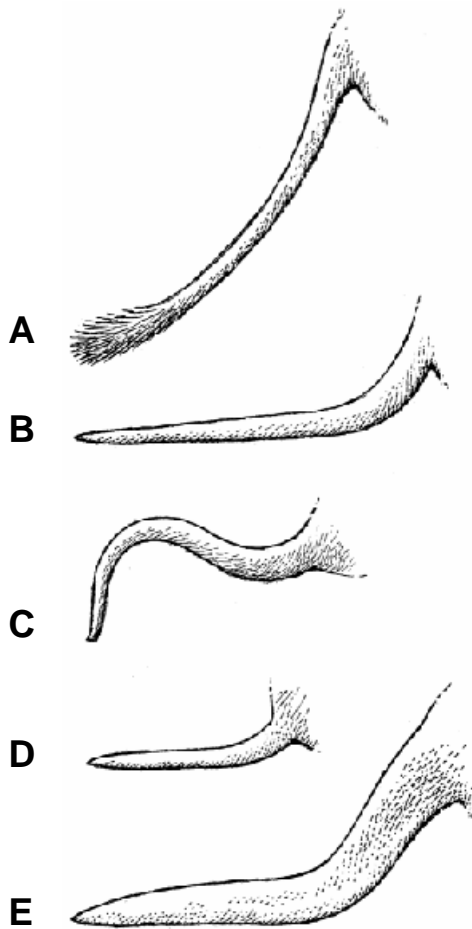
The tail in all macropodids is long, between half and the full head-to-rump length, and may be slender and untapered or proximally robust, depending on its function (Fig. 29.3). It is never particularly long-haired or adorned and does not play a 'fly-whisk' role as it does in some large ungulates. Nor, in contrast to the tails of most extant potoroids, can macropodids use their tails to carry bedding.

The forelimb retains a simple manus with five digits of equal length radiating from a near- circular palm. No digits are opposable, but the manus can grip herbage and they are used sometimes in this way in feeding. They are not modified for digging as are those of extant potoroids.

The hind feet are greatly elongated, have a narrow plantar surface and lack the first toe. The second and third toes are syndactylous, joined for most of their length, but retaining separate claws. They are very small, take no part in support or propulsion, but are used in grooming (especially of the ears and neck). The fourth toe is the largest, while the fifth (outer toe) is of variable size. Thus, like the ungulates, the macropodids have reduced the number of propulsive toes. In some extinct *Sthenurus* species (Rich, van Tets & Knight 1985) simplification went further, producing a kangaroo with only one large, propulsive toe (the fourth) on each pes.

Figure 29.3 Tail shapes, proportions and uses: **A**, long cylindrical balancing tail of tree-kangaroos and rock-wallabies; **B**, tapered, long, but not supportive, tail of smaller *Macropus* species, Swamp Wallaby and pademelons; **C**, recurved tail of *Dorcopsis* and *Dorcopsulus*; **D**, short tail of the Quokka; **E**, stout tapering tail acting as a fifth limb in larger *Macropus* species. (© ABRS) [F. Knight]

Macropodid species vary in size from species weighing 1–2 kilograms to those in which males may reach 90–100 kg. Head-to-tail length at the extremes of this weight range are approximately 700–2500 mm. Body form is related to body size, habitats, locomotion and way of life.

Locomotion in macropodids (Windsor & Dagg 1971) is more varied than the quadrupedal series of stand, walk, trot, canter and gallop typical of ungulates and which involve only variations in scope and sequence of movement of the four limbs. Macropodids may crouch or stand on all four feet or on the pedes only, with or without the support of the tail. They may move in a four-footed

crawl (Fig. 29.1a), feet of each limb girdle moving in synchrony (as in a slow gallop) with the support of the tail in the larger species, or hop with tail and forefeet off the ground (Fig. 29.1b & c), the body between horizontal and nearly upright, propelled by synchronous thrusts of the hind limbs. Tree-kangaroos may also climb using their long and heavily-muscled forelimbs to grasp and pull. Their pedes are shorter and broader than in most other macropodids. Unusually, they move their hind limbs asynchronously when walking along branches. Rock-wallabies have slightly shortened pedes with blunt, robust claws and, like the tree-kangaroos, have long, cylindrical tails (Fig 29.3), well furred to the tip. In these species the tail helps maintain balance when the animals are moving with speed and agility in their three-dimensional environments. The small and medium-sized species which live and move in dense cover have shorter hind limbs and carry the body horizontally, even when hopping rapidly. Their usual posture is a hunch-backed crouch, reminiscent of ungulates of dense cover such as duikers. Such species have relatively short and sparsely haired tails, most exaggeratedly shown in the Quokka, (Fig. 29.3). In the largest species, the comparatively short tail (Fig. 29.3) is heavy and robust at the base, tapers distally and is used as a prop, carrying part of the animal's weight when standing or crawling. Only in these species is it used as support by a fighting male while kicking at an opponent. In these large species, the ears are large, the neck relatively long and the hind limbs, especially the shanks, are particularly long.

Dimorphism in macropodid species is also related to size (Jarman 1983). The smallest species are homomorphic, the largest strongly heteromorphic. In the latter species, males (and sometimes females) grow throughout life, although at a decelerating rate. There is an exaggerated growth of the forelimbs, which become proportionally longer and more robust with larger hands and claws than those of females. The musculature of the pectoral girdle increases and large males become comparatively broad-chested and wide-shouldered. Since much fighting (see below) involves forelimb wrestling, these changes are an exaggeration of weaponry and the degree of exaggeration increases with the species' body size (Jarman 1983). In the three largest species, the Red Kangaroo, and the Eastern and Western Grey Kangaroo, a female at first oestrus may be mated by a male six times her weight. Even a large female will be only a quarter or a third of her mate's weight, making these (and not the often cited elephant seals, *Mirounga* species) the most heteromorphic mammals.

There are only slight differences in coloration between the sexes, except in the Common Wallaroo and the Antilopine Wallaroo, *Macropus antilopinus*, and the Red Kangaroo (in which the colour dimorphism is frequently reversed). In these species, unlike the colour- dimorphic ungulates, the sex-specific coloration is present throughout life and is not assumed by males only upon social maturation.

Body Wall

Macropodids have generally thin skin, compared with vombatids or ungulates. This thinness is exaggerated on the inner surfaces of the limbs, especially of the forelimbs, where a copious subcutaneous venous blood supply associated with the thin skin allows the animals to lose heat by evaporating saliva which they lick onto those parts of the arms (Needham, Dawson & Hales 1974). Similarly, thin skin and evaporation of saliva contribute to the thermoregulation of the scrotum and testes.

The skin of males is thickened in those areas where they risk injury in fighting: the neck and shoulders of most species and the belly in the large species which rear up on their tails and kick at each other's abdomen (P.J. Jarman, unpublished data). The skin also is thickened and heavily keratinised on the plantar surfaces

of the feet; that on the pes usually has a granular surface and this is exaggerated in species living in rocky habitats such as rock- wallabies and wallaroos. The skin of the ventral surface of the tail is thickened in larger species.

The skin of the large macropodid species examined by Mykytowycz & Nay (1964) consisted almost entirely of the papillary layer, the reticular layer being almost non-existent.

Female macropodids have four teats on the abdominal wall within the pouch. When first everted at puberty, these grow to a few millimetres in length. A teat enlarges when suckling a juvenile until, at weaning, it is about the palate length of the young-at-foot (that is, up to 90 mm in the largest species) and can be pulled out of the pouch by the juvenile who sucks while standing outside the pouch. After weaning, the teat regresses, but remains larger than unsucked teats. The pouch of an adult female typically contains teats of different sizes; each juvenile sucks only one teat. Males lack teats.

Macropodids have eccrine sweat glands on the hairless surfaces of their paws and feet (Green 1961) and apocrine sweat glands distributed over the rest of the body surface (Green 1961; Mykytowycz & Nay 1964). In larger kangaroos sweating is initiated only during exercise (Dawson, Robertshaw & Taylor 1974). There are also sebaceous glands associated with the hairs and these are particularly abundant in the chest and axiliary region of males, around the cloaca and in the pouch (Mykytowycz & Nay 1964). The oily secretions from these sebaceous glands can be odorous, as in the Western Grey Kangaroo and the Swamp Wallaby, *Wallabia bicolor*, and may affect the male's appearance and even colour. Their role in male behaviour is discussed below.

Open paracloacal glands of two types are found within the cloaca: a holocrine, sebaceous type and a cell-secreting type (Green 1961; 1963b). Their functions are not understood.

Macropodid fur is generally 15–50 mm deep and consists of abundant, fine, usually straight hairs which are cylindrical or slightly ovoid in section. There are few guard hairs. No macropodids have the sparsity, sleekness or coarseness of fur found in some (especially tropical) ungulates. Nor do any of the medium or large species shed hair when attacked, as do some potoroids. The hair follicles are arranged in groups, each follicle containing a hair and a sebaceous gland surrounding one central follicle which additionally has a sweat gland (Mykytowycz & Nay 1964). Hair follicles are densest on the dorsal and sparsest on the ventral body surfaces. Hairs are finest where the fur is most dense. Fibre diameter varies between species, being especially thin in the densely furred Red Kangaroo. Hairs on the underside of the tail and along the edges of the soles of the feet are stiff and bristle-like. Apart from the large vibrissae (whiskers) in rows on the muzzle, there are a few finer whiskers on the cheeks below the eyes, above the eyes and at the front of the lower jaw. Macropodid species differ in the reflectivity of their fur. The arid-adapted, plains-dwelling Red Kangaroo has more reflective fur, especially on the flanks, than does the Common Wallaroo which lives in the same region, but shelters from the sun in caves or under rock overhangs (Dawson & Brown 1970). The relatively deep, fine fur provides insulation comparable to that of eutherians (Dawson & Brown 1970). The direction in which the hairs lie is, as expected, away from the crown of the head, the midline of the back and a 'crown' in the lumbar region of the back and towards the midline of the chest and belly, with convergence lines across the pectoral region of large males.

Claws on the manus are all similar in size and shape: elongate, laterally compressed, down-curved, tapered and projecting well beyond the pads of the digits. Those on the pes are diverse. On the second and third toes they are small, similar to the manus claws, but more compressed and used only for grooming. On the fourth and fifth toes the claws are short, robust and blunt.

Nail-tail wallabies, genus *Onychogalea*, carry a short, blunt, conical 'claw' on the tip of the tail.

Skeletal System

The modifications of the typical metatherian skeleton characteristic of the Macropodidae relate mainly to a specialised gait or diet and concern the hind limbs or teeth (Fig. 29.4). Relative to the rest of the skeleton, the femur, tibia and fibula and pes are elongated. The tibia and fibula are closely in contact and the fibula is reduced distally to a thin splint. The patella is absent and the load-bearing calcaneum is elongate and strongly developed. The astragalus makes little contact with the navicular (Fig. 29.5). The articulations of the astragalus and tibia and the astragalus and calcaneum are such that movement is confined to the antero-posterior plane (that means the foot can move back and forth only; it cannot twist sideways). This is achieved partly by an expansion of the lateral process on the calcaneum to increase contact with the cuboid. The rest of the elongate pes is dominated by the large metatarsals; the fourth is the largest, the fifth rather smaller (very small and slender in the Red Kangaroo up to almost as long and robust as the fourth in tree-kangaroos) and the second and third are slender and closely adherent. The first metatarsal, like the first toe, is missing. The elongation of the fourth, rather than the third, phalanx distinguishes macropodids and other syndactylous marsupials from most other mammals.
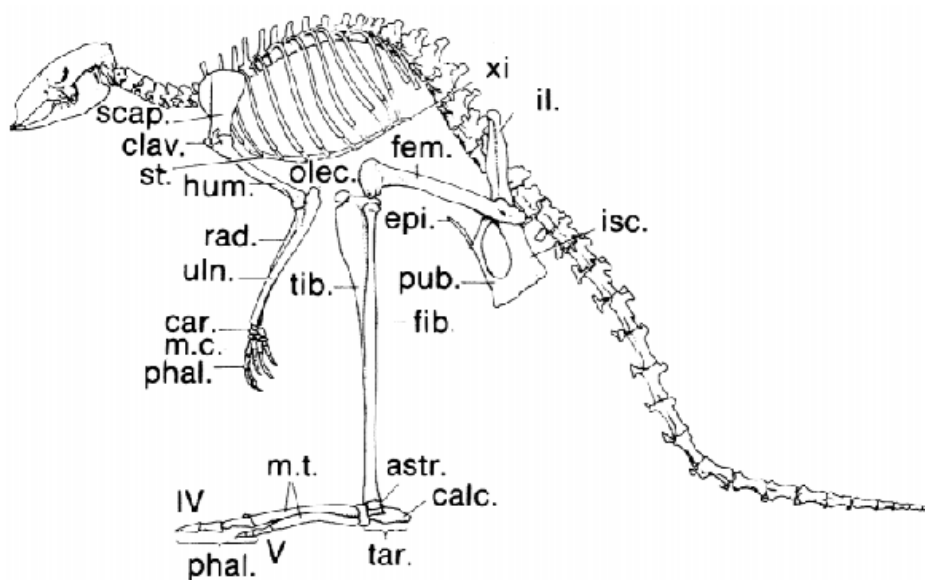

Figure 29.4 Lateral view of the skeleton of a macropodid. astr. = astragulus; calc. = calcaneum; car. = carpals; clav. = clavicle; epi. = epipubic bone; fem. = femur; fib. = fibula; hum. = humerus; il. = ilium; isc. = ischium; m.c. = metacarpals; m.t. = metatarsals; olec. = olecranon process; phal. = phalanges; pub. = pubis; rad. = radius; scap. = scapula; st. = sternum; tar. = tarsals; tib. = tibia; uln. = ulna; xi. = xiphoid. (© ABRS)   [M. Thompson]

The pelvic girdle is not abnormally large or robust and the epipubic bones are proportionately small, but fully ossified. Numbers of vertebrae and ribs are those typical of mammals. The forelimb girdle is unexceptional, save for an epicondylar foramen penetrating the distal end of the humerus. Radius and ulna are separate and of similar thickness; both articulate with the humerus. The simplicity of the hand and wrist is in stark contrast to the specialisation of the

hind foot and ankle and emphasises the very different locomotor and load-bearing roles played by fore- and hind limbs. Since growth is more or less persistent in macropodids, the epiphyses of the limb bones remain unfused.

Figure 29.5 Details of the skeletal structure of the right pes and ankle of *Macropus*. (© ABRS)   [M. Thompson]
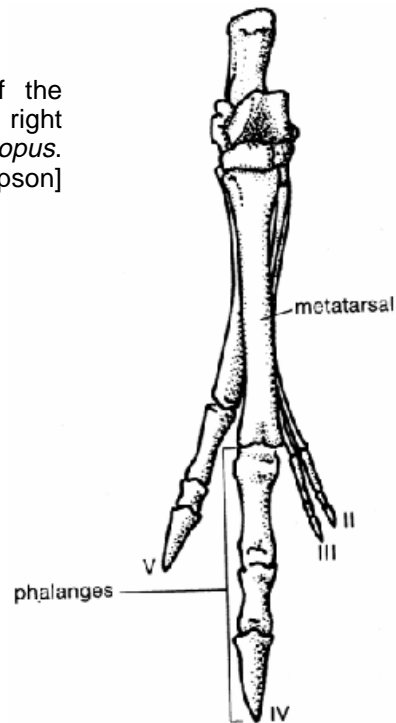
The form of the clavicles and sternum is closely similar to potoroids and phalangeroids. The clavicles are relatively short, robust and strongly curved in large kangaroo species, but slighter and straighter in small species. The sternum consists of five or six segments, to which the clavicles and ribs have cartilaginous attachments.

The distinctively macropodid features of the skull (Fig. 29.6) are largely dental, although members of the family display some metatherian characteristics particularly well, such as the development of palatal vacuities in some species. A deep masseteric canal and masseteric foramen which allows the masseter muscle to gain deep insertion in the dentary also is a distinctive feature of macropodoids and best displayed in the macropodids.

The dental features of note include:

(a) reduction of upper incisors to three blade-like teeth, arranged in a U- or V- shaped arcade;

(b) diprotodonty in the lower jaw; the two procumbent incisors, by far the largest teeth in the mouth, lie as a pair of blades edge-to-edge. Their tips fit within the upper incisor arcade and press against a pad on the front of the palate. This is in contrast to the other families of diprotodont metatherians in which lower and upper incisors occlude at least in part;

(c) reduction or loss of the upper, and absence of the lower, canines, leading to a fully opened diastema in each jaw;

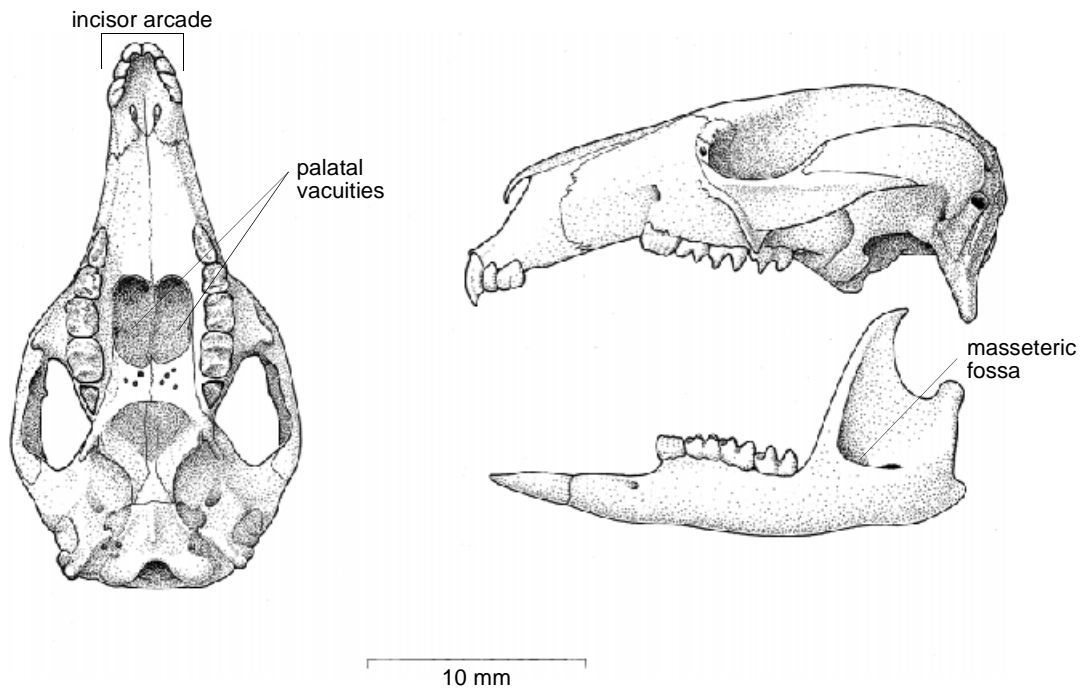(d) two deciduous premolars, one persistent premolar and four molars in each jaw.

Figure 29.6 A typical skull of *Macropus* showing palatal vacuities, masseteric fossa and incisor arcade. (© ABRS)   [G. Milledge]

The molars are robust, generally high-crowned, rectangular teeth with two transverse lophs (ridges) separated by a deep trough; this is crossed by a longitudinal ridge, weakly formed in browsing species but strong in grazers. Full descriptions of the teeth may be found in many publications; Sanson (1978) gives a useful summary.

The molars erupt sequentially at the back of each jaw, changing position relative to the back of the jaw both through elongation of the growing dentary or maxilla and through forward migration of the tooth. When heavily worn, the molar is shed in larger macropodids; in such species the persistent premolar is normally molariform and is usually also shed when worn. Those species with a sectorial premolar, however, retain it and usually all their molars as well. This latter mode characterises browsing and small macropodids. The former is represented by the large, grazing kangaroos (Sanson 1978). Kirkpatrick (1978) describing the development of teeth in macropodids. The serial replacement of worn molars is an adaptation to a diet of abrasive grasses and is unique among metatherians, but is also known in some eutherians (such as elephants).

Locomotion

The two gaits used by macropodids on land are pentapedal locomotion and bipedal hopping. In pentapedal locomotion the tail is used, with the forelimbs, as the third leg of a tripod to support the animal while the large hind limbs are moved forward (Fig. 29.1a). In low-speed hopping (Fig 29.1b), the tail assists balance, but neither the tail nor the forelimbs provide support. The number of hops per minute is almost constant between speeds of 15–35 km/h; increased speed results from longer strides. High-speed hopping, between 40–50 km/h requires still longer strides, but also faster hopping (Dawson 1977).

The energetics of these different forms of terrestrial gait are described in Chapter 17. In water, the hind limbs are moved independently and alternately as a kangaroo swims.

Feeding and Digestive System

All macropodid marsupials are herbivores. The main site of microbial digestion is in the forestomach (see Chapter 17). The browsing macropodid species are distinguished morphologically from grazers mainly on the basis of their dentition. The molars of browsers lack the strong links of the grazers, so that the surface area of contact of upper and lower molars during chewing is increased and the crown appears flatter.

There are also differences in gastric morphology. The sacciform region of the forestomach of browsers tends to be relatively larger than that of grazers. In grazers, the tubiform region is the largest gastric region (Fig. 29.7). This difference in gastric morphology is related to differences in fibre content of the respective diets. The fibre content of grasses is often much higher than that of browse. The large grazing macropodid species, the Red and Grey Kangaroos as well as the Common and Antilopine Wallaroos, appear to be ideally adapted to maintaining their feed intake as grasses mature during dry periods and increase in fibre content. This adaptation is demonstrated in Fig. 29.8.
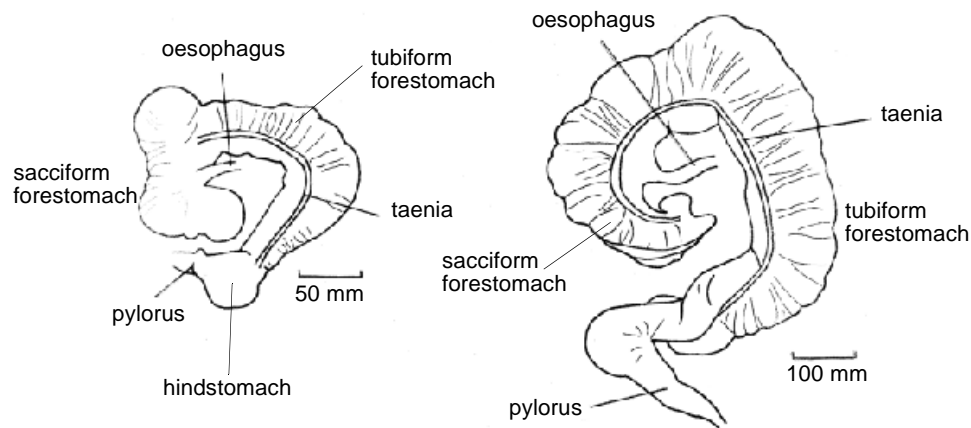

Figure 29.7 Gastric morphology of: **A**, Red-necked Pademelon; **B**, Eastern Grey Kangaroo. (© ABRS)   [K. Hollis]
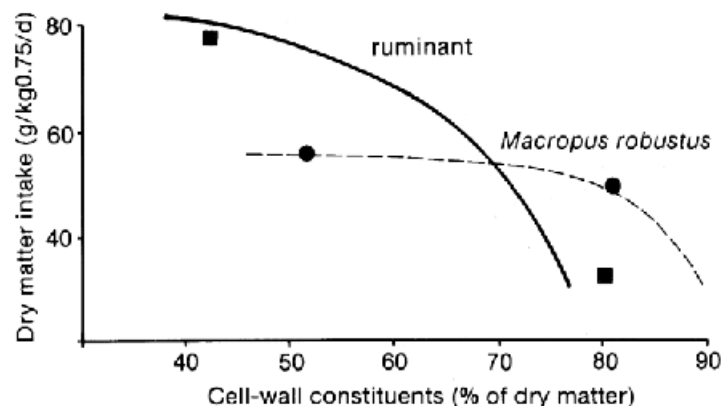

Figure 29.8 Relationship between dry matter intake by ruminants (solid line) and Common Wallaroo (broken line) and fibre content of forage measured as cell-wall constituents.

The solid line on the graph represents the relationship found by Van Soest (1965) between feed intake by ruminants (sheep and cattle) and increasing fibre content of a range of North American forages; as the fibre content increases feed intake declines at an ever increasing rate. The squares represent the feed intakes of sheep fed a low-fibre diet (chopped lucerne hay) and a high-fibre diet (chopped oaten straw) (Hume 1984); they fall close to Van Soest's line. The circles represent the feed intakes of Common Wallaroos fed similar diets. On the low-fibre diet, the wallaroos ate about 30% less than the sheep. This difference reflects the lower maintenance energy requirements of marsupials (Hume 1982). On low-fibre diets intake is limited primarily by metabolic factors, in this case energy requirements.

On higher-fibre diets, however, feed intake by ruminants is limited primarily by gut distension, mainly in the forestomach (in this case the rumen). Coarse feed particles are retained in the rumen for very long periods, restricting further feed intake. Gut distension in grazing macropodids is not as important a factor limiting intake of fibrous feeds because the 'colon-like' tubiform forestomach does not retain coarse feed particles as the rumen does. On the chopped oaten straw diet wallaroos were able to maintain more-or-less a constant rate of passage of food residues through the stomach. As a consequence, feed intake fell only slightly (Fig. 29.8) and was about 50% greater than that of the sheep.

The large grazing kangaroos are thus superbly adapted to survival on poor quality grasses. Browsers do not show this adaptation to the same extent because the tubiform region of the forestomach is not as well developed (Fig. 27.9).

The reader is referred to Chapter 17 for information on the circulatory, respiratory, excretory and nervous systems.

Endocrine System

Reproductive and associated systems. The general structure and function of macropodid endocrine glands are similar to those of other metatherian families (see Chapter 17). Because of the close relationship between various endocrine tissues and the process of reproduction (for example, the hypothalamus, pituitary, pineal, the corpus luteum, interstitial tissue and follicles of the ovary, the testis and placenta), much of the information on their structure and function in macropodids has been integrated into subsequent sections on reproduction and embryology. Only structural and functional aspects of these tissues which are not covered in these later sections are included here.

Hypothalamus. The macropodid hypothalamus has received little attention. Most information about its secretory activity has been obtained indirectly. There is little reason to believe, however, that the basic principles of eutherian hypothalamic function are not equivalent in macropodids or, indeed, in the Metatheria in general. Passive immunisation of the Tammar Wallaby against the hypothalamic gonadotrophin releasing hormone (GnRH), for example, causes inhibition of follicular development during pregnancy, postpartum oestrus and ovulation (Short, Flint & Renfree 1985). This evidence supports the idea that the hypothalamus, through the influence of GnRH, has a trophic effect on the macropodid pituitary. Other groups of releasing hormones presumably will be discovered in the macropodid hypothalamus. The hypothalamus of the Tammar Wallaby also contains the opiate, β-endorphin (K. Gordon, unpublished observation) and presumably also the other brain peptides described for Eutheria.

A typical mammalian organisation of the hypothalamus and pituitary axis has been found in the Tasmanian Pademelon, *Thylogale billardierii* (J.I. Johnson 1977), and, in lesser detail, in the Tammar Wallaby (Renfree *et al*. 1982a). The

macropodid hypothalamus is located between the following coordinates: the preoptic region, optic chiasma, anterior commissure and medial mammillary nucleus.

Pituitary. The neurohypophysis receives axons from the neuronal cell bodies in the hypothalamus and those in the supraoptic and paraventricular nuclei. Active principals with vasopressor and oxytocic effects were first identified in neurohyophyseal extracts from Quokkas and Red Kangaroos (Ferguson & Heller 1965 Heller 1973 McDonald & Waring 1979). These substances are arginine vasopressin, lysine vasopressin, phenypressin and mesotocin (Chauvet *et al*. 1981 Chauvet *et al*. 1983). Bioassays also have demonstrated antidiuretic activity in plasma samples from field and laboratory populations of macropodids (Bakker & Bradshaw 1978 Bentley & Shield 1962). The effect of oxytocin on the myometrium, parturition and milk ejection in macropodids is discussed under reproduction.

Although there is a rapidly expanding body of knowledge on pituitary function in macropodids (Farmer *et al*. 1981 Gallo *et al*. 1978 Hearn 1975a, Purves & Sirett 1959, Tyndale-Biscoe & Evans 1980, Tyndale-Biscoe & Renfree 1987), little is known about the structure of the adenohypophysis in macropodids. Ortman & Griesbach (1958) describe the pituitary histology of the Red-necked Wallaby. More recently, Leatherland & Renfree (1983b) identified three zones in the pars distalis of the Tammar Wallaby based on the distribution of somatotrops, mammotrops, gonadotrops, corticotrops and thyrotrops.

Adrenals. The adrenal structure in macropodids is similar to that of other metatherian and eutherian species (see chapter 17). Comprehensive accounts of adrenal structure in macropodids are given by Bourne (1949) and Jones (1957) and of adrenal development in the Tammar Wallaby by Call, Catling & Janssens (1980).

Both adrenals are enclosed in a strong capsule (Kolmer 1918) and closely associated with the antero-medial surface of the corresponding kidney. The cortex accounts for about half of gland volume and contains a typical mammalian zonation, though this appears less distinct than in the Potoroidae.

Unilateral adrenalectomy results in hypertrophy of the remaining adrenal within 10 days, mostly caused by enlargement of the zona fasciculatus (Reid & McDonald 1968a). Enlargement of the zona glomerulosa in alpine Eastern Grey Kangaroos when compared with coastal populations (Scoggins *et al*. 1970) is thought to reflect an adaptive response to sodium deficiency in alpine environments.

Few studies have been made on adrenocortical function in macropodid marsupials or the metabolic actions of adrenocortical steroids (see McDonald 1977 for a detailed review). Ablation of the adrenals in the Red Kangaroo causes similar effects to those seen in eutherians, such as muscle weakness, anorexia, hyponatremia and hyperkalemia (McDonald 1974). Such animals can be maintained on daily intramuscular injections of corticosteroids (McDonald 1977).

An adrenal-related function peculiar to some macropodids is an insensitivity to the diabetogenic and nitrogen-mobilising actions of glucocorticoids (Fig. 29.9) (Griffiths, McIntosh & Leckie 1969b, McDonald & Bradshaw 1981), a function which may be an important adaptation for arid zone species (see McDonald 1977, McDonald & Waring 1979). In Quokkas, ACTH causes a minor transient increase in urinary nitrogen excretion in both sexes which rapidly declines during treatment. Cortisol has no effect on fasting plasma glucose levels, but causes a small rise in the hypoglycaemic effect of insulin and nitrogen excretion, probably due to increased renal clearance rather than tissue nitrogen metabolism (McDonald & Bradshaw 1981). Exceptions to this pattern include the Tammar

Wallaby, which is sensitive to the diabetogenic activity of glucocorticoids (Cooley & Janssens 1977, Janssens & Hinds 1981) and efficiently conserves nitrogen in nitrogen deficient habitats (Kinnear & Main 1976).
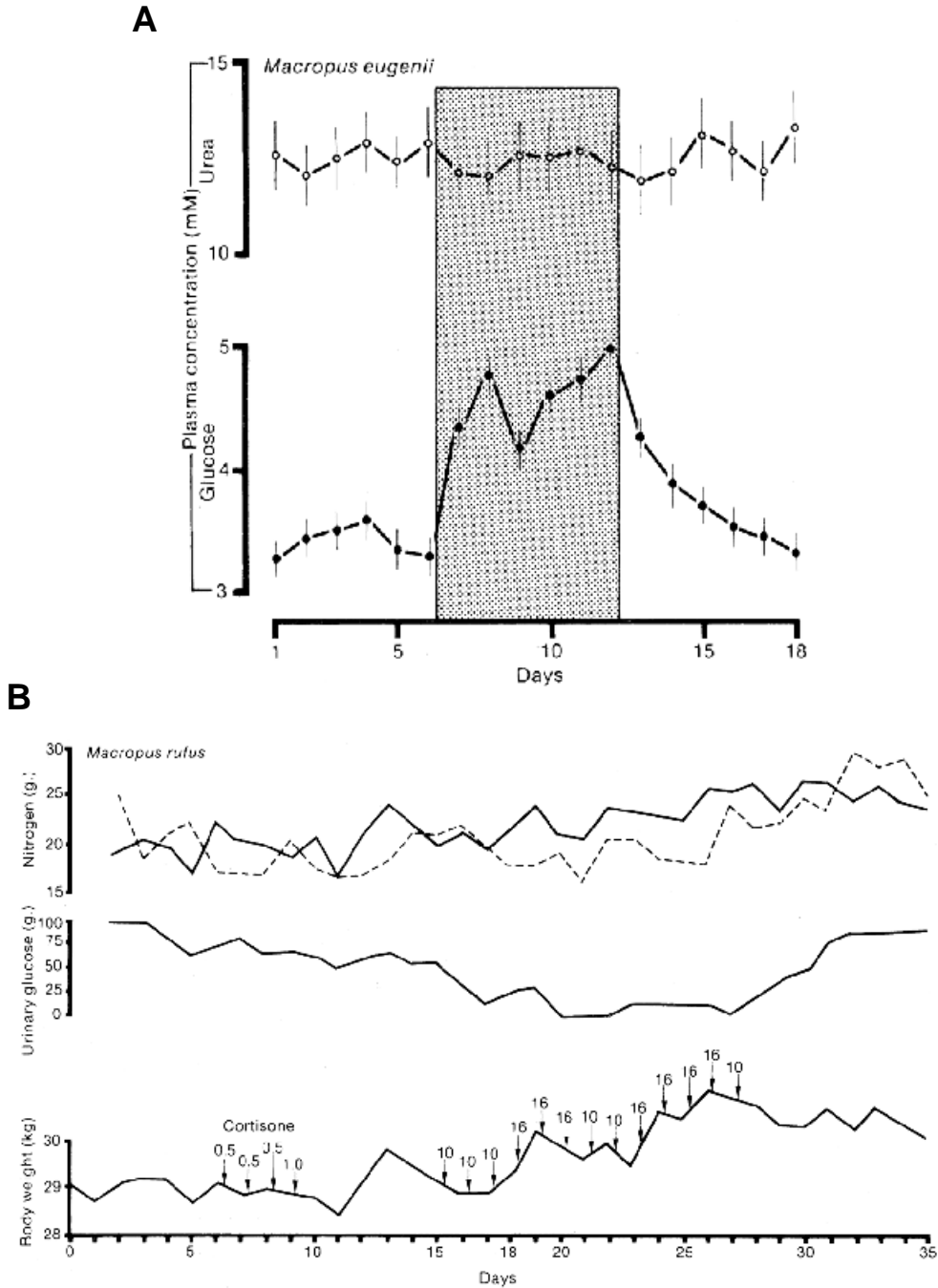
Figure 29.9 Comparative diabetogenic and nitrogen-mobilising activities of glucocorticoids in macropodids: **A**, mean plasma concentrations of glucose and urea (±S.E.M.) in six normal male Tammar Wallabies before, during (hatched area) and after treatment with 10 mg kg^{-1} per day of cortisol showing a diabetogenic response during period of cortisol infusion, indicated by shaded area (after Janssens & Hinds 1981); **B**, insensitivity of a diabetic male Red Kangaroo to the effects of cortisone acetate on nitrogen balance (solid line, N intake; dashed line, N excretion) and glycosuria. Cortisone (0.5-1.0 g per day) and insulin (units) injections indicated by arrows. (After Griffiths *et al*. 1968)

Corticosteroid secretion from the macropodid adrenal is controlled by secretion of ACTH from the pituitary (McDonald 1977, McDonald & Waring 1979). Synthetic and porcine ACTH are equipotent in the Quokka (McDonald & Bradshaw 1978), but much less effective than in *Trichosurus* species or humans. Cortisol is the major corticosteroid secreted by the adrenal in the Quokka, but corticosterone makes up between 25 and 50% of the total.

Environmental conditions affect adrenal structure in Red Kangaroos. Severe drought causes reduced adrenal size, cortical folding and nodulation and shrinkage of the three zones of the adrenal cortex with a concomitant accumulation of lipids in cortical cells. These changes are associated with significant changes in the size of the pituitary, but there is evidence of continued stimulation of the zona fasciculata and glomerulosa (Myers, Bailey & Dudzinski 1976).

Pancreas. The pancreas contains typical exocrine and endocrine components found in other metatherian and eutherian mammals. Groups of cells corresponding to the insulin-secretion islets of Langerhans have been identified in various macropodid species (White & Harrop 1975). Injection of insulin causes rapid onset of hypoglycaemia in macropodids, as occurs in other mammalian species. Alloxan treatment in Quokkas (Barker 1961) and Red Kangaroos (Griffiths *et al.* 1968) causes typical degeneration of insulin secretion cells in the islets of Langerhans resulting in the development of diabetes mellitus. Resistance to the diabetogenic actions of glucocorticoids in all macropodids studied suggests that a different mechanism controls insulin action than the standard eutherian controls.

Thyroid. Except for the brief anatomical descriptions of Mackenzie & Owen (1919b), there are no structural studies of the macropodid thyroid or parathyroid. More is known, however, about macropodoid thyroid hormones and their functions. Thyroxine and triiodothyronine are known to compete for binding sites on macropodid plasma proteins and free thyroxine concentrations in the plasma of the Tammar Wallaby and the potoroid Long-nosed Potoroo, *Potorous tridactylus*, are similar to those found in eutherians (McDonald & Waring 1979).

Thyroid hormone secretion rates in Tammar Wallabies are similar to those recorded in eutherian species and significant increases in total and free plasma thyroxine concentrations occur during cooler winter months. Steroids affect thyroid activity in the Tammar Wallaby.

The importance of the thyroid in development of thermoregulation in macropodids has been shown by Setchell (1974a) in studies of Tammar Wallabies pouch young. The transition from ectothermy to endothermy in this species occurs between days 140–180 of pouch life and is associated with an increase in thyroid size, coinciding with increased uptake of radio labelled iodine by the gland (Fig. 29.10a), the appearance and growth of hair and the development of the ability of pouch young to elevate oxygen consumption in response to low ambient temperatures (Fig. 29.10b). By day 180 of pouch life, oxygen consumption at 20°C is about twice that at 35°C.

Other endocrines. A renal juxtaglomerular apparatus similar to that found in other mammals is present in at least some macropodids and a renin-angiotensin system has been identified in various kangaroo species (Simpson & Blair-West 1971, Blair-West & Gibson 1977).

Other endocrine systems which may have functional significance, such as those associated in eutherians with the gastrointestinal tract and urinary system, have not been identified or studied in macropodoids.
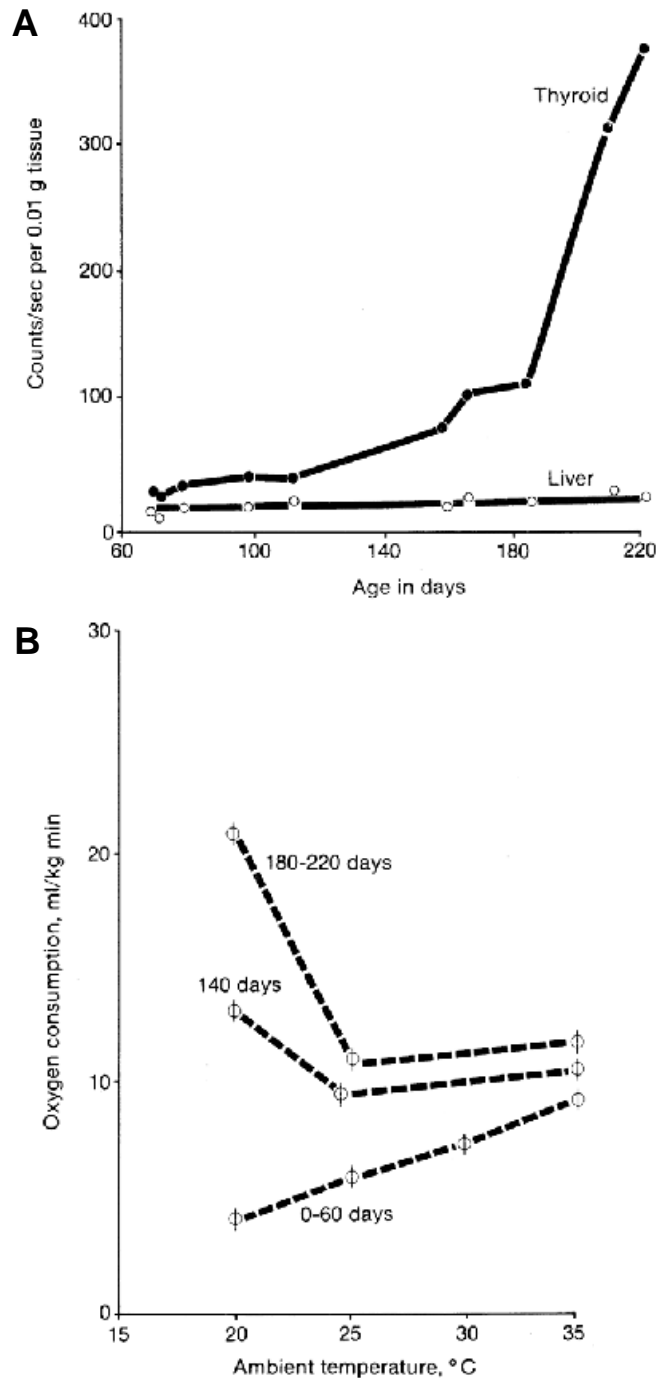
Figure 29.10 Thyroid function and the development of endothermy in Tammar Wallaby pouch young: **A**, changes in I[131] uptake by the thyroid of ten Tammar Wallabies aged 65-220 days showing a rapid increase in thyroid activity in pouch young after about 180 days; I[131] uptake by the liver during this period is included for comparison; **B**, oxygen consumption (ml kg^{-1} min^{-1}) by three age groupings of Tammar Wallaby pouch young during the transition from ectothermy (0-60 days) to endothermy (180-220 days). The associated increase in thyroid activity is shown above. (After Setchell 1974a)

Exocrine System

The exocrine functions of the male and female reproductive systems of macropodids, including the mammary gland, are described below. This section describes the structure and function of those exocrine glands of cutaneous origin, for example salivary glands, sweat glands and scent glands.

Salivary glands. Three pairs of major salivary glands are present in macropodids (Parsons 1896, Forbes & Tribe 1969). The parotid glands of most macropodid species, like their eutherian herbivore counterparts, are large (Forbes & Tribe 1969) and the submandibular glands are relatively small. Histologically, the parotid is serous, the submandibular glands are mixed, with a large serous component and occasional mucous acini, and the sublingual glands are almost completely mucous. No functional studies exist and there is little known about the composition of the secretion from these glands. Macropodids produce a copious saliva rich in sodium and bicarbonate ions. Unlike eutherian ruminant saliva, macropodid saliva contains an amylase activity (see Tyndale-Biscoe 1973).

Cutaneous glands. Few detailed studies exist on cutaneous glands in macropodids (Bentley 1955, Green 1961, Mykytowycz & Nay 1964, Russell 1985).

The structure and distribution of sweat glands are known in the Quokka (Green 1961) and in various other species of kangaroos and wallaby (Mykytowycz & Nay 1964). In the Quokka, apocrine sweat glands were found in hairy skin and eccrine glands in bare regions (such as paws). Similar distributions of skin glands were reported in the five other macropodids examined by Mykytowycz & Nay (1964). These dense populations of well-developed sweat glands may present a thermoregulatory adaptation for life in semi-arid environments. Signs of profuse sweating in the fur of kangaroos after prolonged chases tend to support this hypothesis. The most developed apocrine glands occur in the axillary and sternal regions. In addition, aggregations of large apocrine glands have been found over the scrotum in males and around the cloaca-pouch area in females (Mykytowycz & Nay 1964). In adults of the three species studied, the sternal apocrine glands are considerably larger in males. In females, the sternal glands are less developed than those associated with the pouch. Unlike the apocrine glands, sebaceous glands in these regions are no larger than in adjacent areas of skin.

The characteristic reddish-brown pigmentation of the sternal patch in adult males and females results from tryptophan derivatives in the apocrine secretion which cause internal pigmentation of the hair and produce a pigment which adheres externally to the hair shafts (Nicholls & Rienits 1971). Seasonal fluctuations occur in the secretory activity of the sternal glands and the amount of sternal pigmentation of some species. At certain times of the year the sternal glands in male grey kangaroos are particularly active and the hair over the sternal region and along the midventral line is matted with a thick, sticky secretion (Mykytowycz & Nay 1964). This may be important for marking, perhaps individual recognition, especially in males, or might indicate reproductive state of the female. Pouch-associated glands may help neonates to locate the pouch after birth and/or may help emergent pouch young in pouch identification.

Paracloacal glands also occur in macropodids. These lie in pairs along the lateral cloacal walls and drain into the cloaca by single, thin-walled ducts. These glands are small and cyst-like, with secretory cells lining the numerous septa projecting radially towards the central lumen. They produce a thick, oily, sometimes cellular, secretion which mixes with faeces and urine in the cloaca. A pungent odour has been reported from these glands in some species (Russell 1985).

A single pair of cloacal glands occurs in most species, and although there are no detailed studies on their function, they presumably play a role in social behaviour. Specialised frontal, ear, lachrymal or labial glands have not been identified.

Reproduction

Genetics. The most common chromosomal complements of the Macropodidae are N=16 or 22. Variations are seen in the Swamp Wallaby (male N=ll, female N=10); tree-kangaroos (N=12 or 14, depending on species); the New Guinean Macleay's Dorcopsis; the Unadorned Rock-wallaby; and the Short-eared Rock-wallaby, *Petrogale brachyotis* (N=18); the Brush-tailed Rock-wallaby; the Northern Nail-tail Wallaby, *Onychogalea unguifer* and the Red Kangaroo (N=20); and the Banded Hare-wallaby, (N=24) (Hayman 1977).

Reproductive anatomy & control of reproduction: Female. The macropodid female reproductive system is like that of other marsupials (see Chapter 17) and will not be discussed in this account. A patent birth canal is retained after the first parturition (Fig. 29.11a). All macropodid species studied are monovular and polyoestrous with cycles of 22–46 days (Table 29.1) (Tyndale-Biscoe 1984, Tyndale-Biscoe & Renfree 1987). There is a clearly defined proliferative or pro-oestrus phase during follicular growth and maturation. Ovulation is spontaneous and usually alternate. The resulting corpus luteum actively secretes progesterone which controls the development of a luteal or secretory phase in the endometria of the two quite separate uteri. A rather poorly defined post-luteal phase follows as the corpus luteum and uteri regress. In an unmated breeding female, this phase merges with the next pro-oestrus phase and ovulation.

Table 29.1 Comparison of oestrous cycle and gestation lengths, litter size and the number of corpora lutea present in a variety of macropodoid species. [Table compiled from Tyndale-Biscoe 1986]

SPECIES	OESTROUS CYCLE (days)	GESTATION (days)	NUMBER OF CORPORA LUTEA	LITTER SIZE
Aepyprymnus rufescens	21-36	21-30	1	1
Potorous tridactylus	42	38	1	1
Bettongia lesueur	23	21	1	1
Bettongia penicillata	22-23	21	-	1
Bettongia gaimardii	23.2	21.1	1	1
Wallabia bicolor	32.6 ± 3.6	35.5 ± 2.3	-	1
Setonix brachyurus	28	27	1	1
Petrogale penicillata	31(30-32)	31(30-32)	-	1
Macropus eugenii	30.6 ± 1.2	29.3 ± 1.1	1	1
Macropus agilis	32.4(29-34)	29.4(29-33)	-	1
Macropus rufogriseus	31.9	29.4	1	1
Macropus parma	41.8 ± 0.7	34.5 ± 0.1	-	1
Macropus parryi	42.2(41-44)	36.3(34-38)	-	1
Macropus giganteus	45.6 ± 9.8	36.4 ± 1.6	1	1
Macropus fuliginosus	34.9 ± 4.4	30.6 ± 2.6	1	1
Macropus rufus	34.8 ± 0.6	33.2 ± 0.2	1	1

The corpus luteum suppresses follicle growth and ovulation and stimulates development of the luteal phase in the uterus. Inhibition of follicle growth is most pronounced early in the cycle and diminishes to zero by the second half of the cycle, so that follicle growth coincides with decline of the corpus luteum (Tyndale-Biscoe 1963a; Tyndale-Biscoe & Hawkins 1977). Since macropodids are monovular with alternate ovulation, in each pregnancy there is one gravid uterus ipsilateral to the corpus luteum and one non-gravid uterus ipsilateral to the developing follicle. There are numerous recorded unilateral effects of
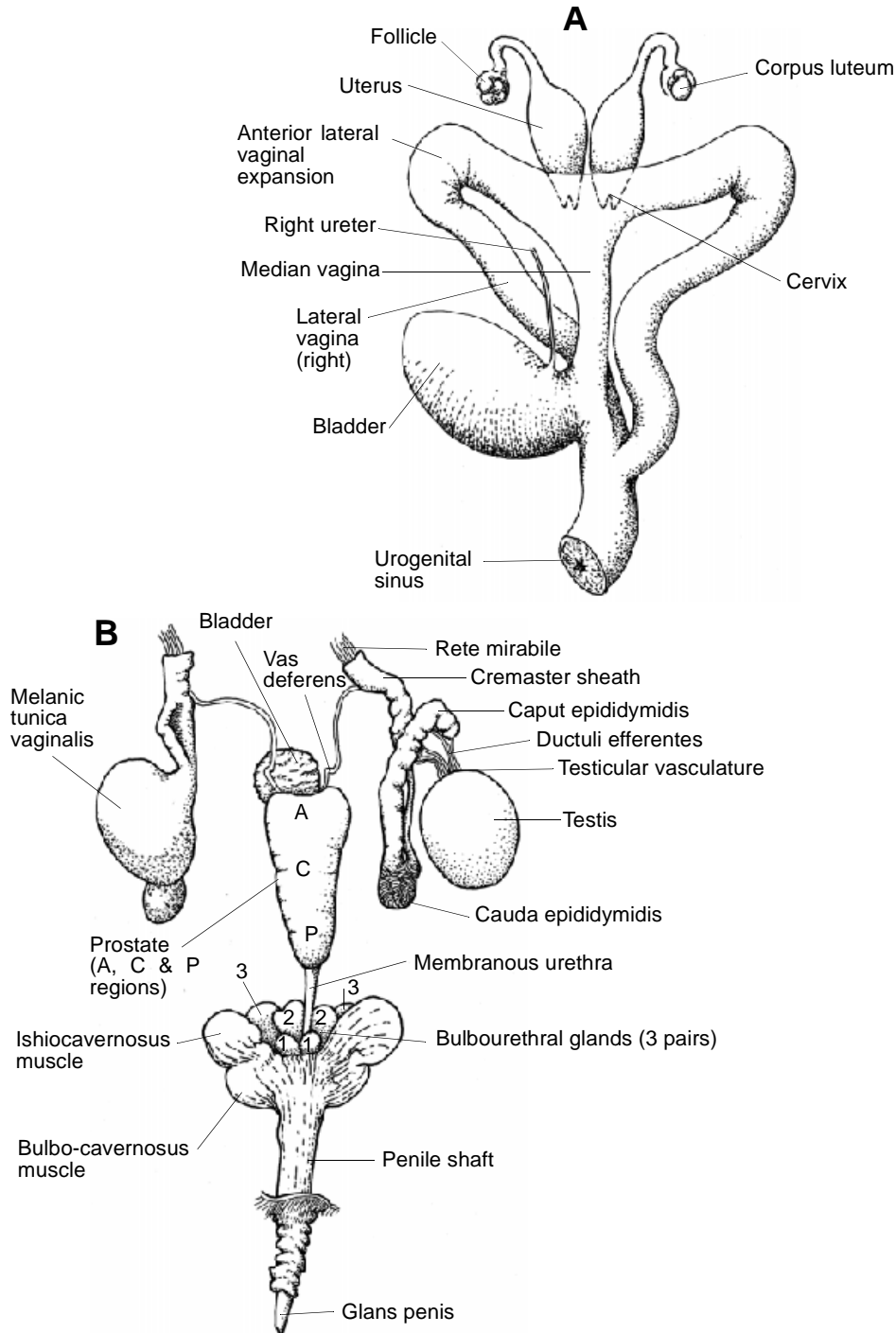
A

Follicle

Corpus luteum

Uterus

Anterior lateral
vaginal
expansion

Right ureter

Median vagina

Cervix

Lateral
vagina
(right)

Bladder

Urogenital
sinus

B

Bladder

Rete mirabile

Vas
deferens

Cremaster sheath

Melanic
tunica
vaginalis

Caput epididymidis

Ductuli efferentes

Testicular vasculature

A

Testis

C

P

Cauda epididymidis

Prostate
(A, C & P
regions)

Membranous urethra

3

3

Ishiocavernosus
muscle

2   2
1   1

Bulbourethral glands (3 pairs)

Bulbo-cavernosus
muscle

Penile shaft

Glans penis

Figure 29.11 A, The reproductive tract of the female Tammar Wallaby. The right ureter is shown passing between the median and right lateral vaginae. The diagram is based on a photograph of an oestrous, newly parturient female. The post-partum uterus is on the left side, ipsilateral to the corpus luteum. A large Graafian follicle (4.0 mm) is present on the right ovary. (After Renfree 1983); **B**, reproductive tract of the male Tammar Wallaby. The left testis and epididymis are shown still enclosed in the melanic tunica vaginalis, with the cauda epididymidis forming a distinct distal bulge, the testicular vasculature (rete mirabile) and vas deferens are shown passing into the prominent inguinal (cremaster) sheath. On the right the tunica vaginalis has been removed to demonstrate the structure and relationships of the testis, ductuli efferentes, rete mirabile, epididymis and vas deferens. The 'carrot-shaped' prostate, divided into its anterior (A), central (C) and posterior (P) segments, is connected to the penile urethra by a membranous urethral segment. The arrangement of the three pairs of bulbourethral glands (1, 2 & 3) is shown in relation to the ischio- and bulbocavernosus muscles. (© ABRS)   [G. Scott]

pregnancy (Tyndale-Biscoe & Renfree 1987), perhaps due to the close association of the ovarian and uterine blood vascular system (Towers, Shaw & Renfree 1986). These observations, together with those noting that the foetus or placenta influences the maternal endocrine system in some way to reduce the time between consecutive oestrus periods when a pregnancy intervenes (Merchant 1976, 1979; Merchant & Calaby 1981), show that macropodid marsupials do have a maternal recognition of pregnancy (Tyndale-Biscoe & Renfree 1987). In the Tammar Wallaby, the reduction in the time between successive oestrus periods appears to be due to an influence by the conceptus on the decline of progesterone and the timing of the pre-ovulatory luteinising hormone (LH) peak which follows less than 24 hours after behavioural oestrus (Tyndale-Biscoe *et al*. 1983).

After conception, one ovary has a single corpus luteum of pregnancy, with primary follicles towards the periphery and secondary or tertiary follicles on the contralateral ovary (Renfree *et al*. 1984) and a homogeneous central mass of interstitial tissue (Tyndale-Biscoe & Renfree 1973a). The ovaries are surrounded by a membranous fimbria. The oviduct is about 20 mm long in the Tammar Wallaby. The uterus, consisting of the outer myometrium and inner endometrium, shows the characteristic cyclical changes dependent on the stage of the cycle or pregnancy (see Chapter 17). The endometrium expands dramatically during pregnancy, but after the first third of the gestation period, only the gravid uterus continues to increase in weight and produce copious secretion (Fig. 29.12c). In Tammar Wallabies, the weight of the endometrium is greater and the composition of the uterine secretions different in non-gravid compared to gravid uteri after 10 days of pregnancy (Renfree 1972b). Since the transfer of a blastocyst to a cyclic, non-pregnant animal, or to the side contralateral to the corpus luteum initiates similar endometrial proliferation, the morphogenetic effect on the uterus must be attributable to the embryo, rather than the corpus luteum, despite increasing peripheral plasma progesterone levels in late pregnancy. (Fig. 29.12).

During embryonic diapause in the Tammar Wallaby, proliferation of the endometrium can be initiated and maintained by injections of exogenous progesterone, but both gravid and non-gravid endometria respond. If progesterone injections are then stopped, only the uterus containing the embryo continues to show the secretory, enlarged endometrium and the non-pregnant uterus degenerates to a state usually observed in the non-pregnant cycle (Renfree & Tyndale-Biscoe 1973a). A similar unilateral response of the uterus to pregnancy has been observed in the Quokka (Wallace 1981; M.B. Renfree, unpublished data).

The lateral vaginae and median vagina respond to late pregnancy and approaching oestrus by becoming highly motile and very vascular. They increase in weight from 4.5–9.0 g (Short *et al*. 1985) and can expand to accommodate relatively large volumes of semen at oestrus.

Reproductive anatomy & control of reproduction. Male. The gross anatomy of the male reproductive system in macropodids (Fig. 29.11b) is similar to that of other metatherians (see Chapter 17). Paired testes and epididymides are located externally in a pendulous, pedunculate, prepenile scrotal sac. The outer surface of the scrotum is lightly furred and endowed with numerous large sweat glands (Mykytowycz & Nay 1964) which assist in the thermoregulatory function of the scrotum. A strong, active cremaster muscle encloses the spermatic cord and retracts the scrotal contents tightly against the pelvic body wall during cold weather or situations of stress. When this muscle is relaxed, for example in warm weather, the scrotum hangs obtrusively. The vasa deferentia are initially intra-scrotal, passing along the medial margin of the epididymides before passing through the scrotal stalk with the vascular contents of the spermatic cord into the pelvic cavity to eventually join the prostatic urethra from behind, close
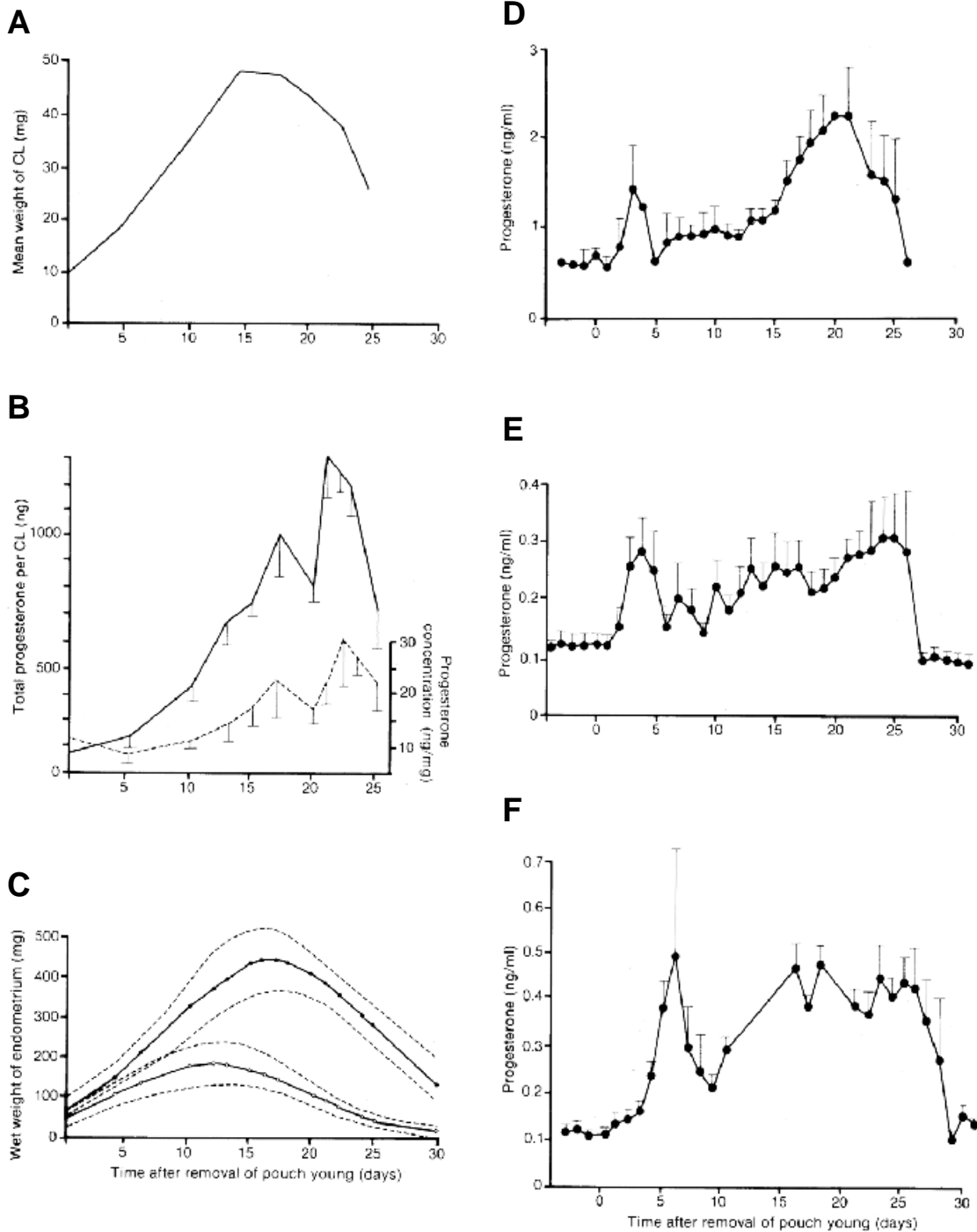
Figure 29.12 Endocrine profiles of female macropodids: **A**, wet weights of the corpus luteum during pregnancy in Tammar Wallabies; **B**, progesterone content and concentrations of corpora lutea of Tammar Wallabies throughout pregnancy (mean ± S.E.). (Data from Renfree *et al*. 1979); **C**, changes in wet weight of the endometria of gravid (closed circles) and non-gravid (open circles) uteri of Tammar Wallabies sampled during pregnancy induced by removing pouch young. Individual values are presented as a weighted quadratic regression with 90% confidence limits for the regression lines (after Renfree & Tyndale-Biscoe 1973a); **D-F** peripheral plasma progesterone profiles during pregnancy for; **D**, Quokka, **E**, Red-necked Wallabies and **F**, Tammar Wallabies. Birth occurs at day 25 in D, and day 27 in E, and F, coincident with the progesterone fall. [D, After Cake *et al*. 1980; E, after Walker & Gemmell 1983a; F, after Hinds & Tyndale-Biscoe 1982]

to the neck of the bladder (Fig. 29.11b). Seminal vesicles and ampullae are lacking in macropodids and two or three pairs of Cowper's (bulbourethral) glands are, with the prostate, the only discernible accessory glands of the male reproductive system (Disselhorst 1904; Fraser 1919; Oudemans 1892; Rodger & Hughes 1973; Rodger & White 1974b; Setchell 1977).

The penis forms an S-shaped structure in a juxta-cloacal sac when in the normal relaxed position. When erect during sexual arousal, and sometimes during aggression, it is protruded by eversion of the sac through the cloacal opening to the exterior, occluding the cloaca. Unlike most other metatherians, the glans is not bifid, but consists of a single vermiform appendage (Fig. 29.11b). The reason for this distinct morphological difference in the macropodids is unknown and it would be interesting to compare the insemination characteristics of macropodids with representatives of other metatherian families exhibiting a strongly bifid glans penis.

The scrotum is discernible at or shortly after birth (Maynes 1973; Poole 1973; M.B. Renfree, unpublished data). Testicular descent is completed by about 90 days postpartum in the Parma Wallaby (Maynes 1973). The incidence of scrotal pigmentation is variable in adult macropodids as in some other metatherian families. In the Eastern Grey Kangaroo, and the Tammar and Red-necked Wallabies the tunica vaginalis is darkly pigmented (Setchell 1977), but in the Red Kangaroo it is unpigmented. The possible relationship of this pigment layer to thermoregulation of the scrotal contents has been discussed elsewhere (Biggers 1966; Harding 1977; Setchell 1977; Temple-Smith 1984a; see also Chapter 17).

Extensive studies, in both conscious and lightly anaesthetised macropodids, demonstrate a temperature differential of 2.5–5°C between body and testicular temperatures (see Setchell 1977). The importance of the rete mirabile in establishing this thermal cline between body and testicular temperature and in pulse elimination in arterial blood reaching the testis was demonstrated by Setchell & Waites (1969) in *M. eugenii*. The numbers of arteries and veins (respectively) in the rete mirabile of macropodids are about 200 and 150 in the Tammar Wallaby, 98 and 110 in the Red-necked Wallaby, 120 and 100 in the Common Wallaroo and 95 and 75 in the Red Kangaroo.

There is nothing particularly remarkable about testicular structure or spermatogenesis in macropodids. The diameter range of the seminiferous tubules are 180–320 µm, depending on species (Poole 1973, Setchell 1977). The tubules are separated by small islands of interstitial tissue containing androgen secreting Leydig cells (Newsome 1973, Setchell 1977) which occupy less than 5% of total testicular volume (Type 2 morphology of Fawcett, Neaves & Flores 1973). There are no studies on the structure of Leydig cells in macropodid species. Testosterone concentrations in the testicular vein of Red Kangaroos and Common Wallaroos are about 80 and 100 ng/ml, respectively, giving testosterone secretion rates of 2.6 and 6.8 ng/min per g testis and 0.15 and 0.4 mg/d (Carrick & Cox 1973). Increased plasma androgen levels in male Tammar Wallabies which were penned with oestrous females (Catling & Sutherland 1980), suggest a stimulation of increased gonadotrophin secretion by the pituitary under these conditions, providing evidence of a possible pheromone effect on reproduction in the males of this species. Testicular receptors for LH and FSH have been demonstrated in macropodids (Stewart, Sutherland & Tyndale-Biscoe 1981) and in five species, *in vivo* injection of GnRH raises plasma levels of testosterone (Lincoln 1978).

The importance of trophic secretions from the pituitary on testicular function is clearly demonstrable in male Tammar Wallabies where plasma gonadotropins are undetectable one week after hypophysectomy and in which paired testicular weights fall from about 40 g to 5.5 g after three months (Hearn 1975a). No maturation stages beyond primary spermatocytes are seen at this time.

Environmental factors affect testicular function in some macropodids. In the Red Kangaroo, spermatogenesis is impaired during times of severe drought. Heat and poor nutrition affect spermatogenesis and these factors appeared to work synergistically to determine the level of impairment to testicular function (Newsome 1973). In comparison to herbivorous eutherians of similar body size (such as sheep), kangaroos are able to maintain normal spermatogenesis at exposure to much higher environmental temperatures (Frith & Sharman 1964; Newsome 1965b).

The process of spermiogenesis in macropodids does not differ greatly from that described in peramelids (Sapsford, Rae & Cleland 1969a) and dasyurids (Kerr & Hedger 1983). Eight cellular associations have been identified in macropodid marsupials (Setchell & Carrick 1973) and the lengths of the spermatogenic cycle in the Tammar and the Red-necked Wallaby are 16 and 17 days, respectively. The duration of the following spermatogenic parameters in these species are: meiotic prophase - 21 and 24 days; spermiogenesis - 25 days each; preleptotene primary spermatocyte to sperm release from the germinal epithelium - 48 and 51 days, respectively.

Rete testis fluid collected from cannulated efferent ducts in the Tammar Wallaby showed a flow rate of 0.0125 mg/g testis/h, which is not significantly different from eutherian rates and contained 8×10^7 spermatozoa/ml, no glucose, inositol or proteins and similar concentrations of sodium, potassium and chloride to eutherian mammals (Setchell 1970).

Macropodid spermatozoa are similar in structure to those of other Australian metatherians, especially the phalangerids (see Chapter 17). They show identical sequences of structural modification during maturation in the epididymis, although development of invaginations of the plasma membrane along the posterior midpiece have not been observed (Harding, Carrick & Shorey 1979). Harding *et al.* (1979) were able to distinguish four macropodoid species (Common Wallaroo, Parma Wallaby, Red Kangaroo and Long-nosed Potoroo) from each other on the basis of minor variations in shape and size of the sperm head and flagellum. The dimensions of sperm from 10 macropodoid species were summarised by Cummins & Woodall (1985): total sperm length varies from 106–123 µm, consisting of 5–9 µm head, 8–15 µm midpiece and 89-116 µm principal piece lengths. The epididymis is typically mammalian in its macro- and microanatomy (Setchell 1977; Jones, Hinds & Tyndale-Biscoe 1984). Morehead & Setchell (see Setchell 1977) identified typical regionalisation of epididymal function, for example, fluid absorption, secretion and sperm storage. Setchell & Carrick (1973) determined the minimum transit time for sperm through the epididymis in Tammar Wallabies to be 13 days. Jones, Hinds & Tyndale-Biscoe (1984) reported principal, basal, mitochondrion-rich and apical cells and intraepithelial leucocytes in the epithelial lining of the ductus epididymis and described six structurally different zones in the initial, middle (three zones) and terminal segments (two zones). These three segments correspond closely to the head, body and tail of the epididymis. Sperm motility first develops in the initial segment, but structural maturation of spermatozoa is first evident in the initial zone of the middle segment. Cytoplasmic droplets detach from spermatozoa in the middle segment and subsequently are phagocytosed in this segment by a specialised zone of epithelial cells, similar to that described in the epididymis of the phalangerid, the Common Brushtail Possum, *Trichosurus vulpecula* (Temple-Smith 1984b). A typically eutherian distribution of spermatozoa was found in the epididymis of four macropodid

species (Bedford, Rodger & Breed 1984) with large sperm reserves located in the caudal region of the epididymis. Hypophysectomy causes rapid regression of the macropodid epididymis (Hearn 1975a, 1977). After 120 days post-hypophysectomy, epididymal weight falls from about 6.5 g to 1.8 g, while the diameter of the ductus epididymidis in the head and tail regions of the epididymis shows concomitant changes (Hearn 1975a).

The macropodid prostate, like that of most other marsupials, is a large, disseminate, carrot-shaped organ (Fig. 29.11b) divisible into histologically discrete anterior, central and posterior segments (Rodger & Hughes 1973; Rodger & White 1974b; Setchell 1977). Studies on the composition of the secretion from each segment in three macropodid species, Tammar Wallaby, Red Kangaroo, and Eastern Grey Kangaroo, showed that these regions are also biochemically distinct (Rodger & White 1974b). High concentrations of glucose were present in the posterior segment of these species, fructose is virtually absent and N- acetyl glucosamine is present in high concentrations, especially in the central segment, where concentrations exceed 450 mg/100 g of prostatic tissue.

Three pairs of Cowper's glands are present in most macropodid species (Rodger & Hughes 1973, Setchell 1977). The structure of these glands is described in Chapter 17, as in other mammals, they produce a thick, clear, viscous mucous secretion rich in sialoproteins (Rodger & Hughes 1973, Hearn 1975a). The exact function of this secretion is unknown, but in eutherians it is thought to act as a pre-ejaculatory lubricant for the urethra. No seasonal changes in these accessory glands have been seen in the Tammar Wallaby, but they show rapid involution following castration or hypophysectomy, confirming their androgen-dependent status (Hearn 1975a, 1977).

Pregnancy. A comprehensive summary of the breeding biology of macropodids is given by Tyndale-Biscoe (1984). Briefly, two features distinguish reproduction in the macropodids from other marsupials. Firstly, a period of lactation-controlled embryonic diapause of variable duration may occur after blastocyst formation and, secondly, the duration of pregnancy is protracted to occupy the full length of the oestrous cycle. Unlike in eutherians, however, the life-span of the corpus luteum does not extend much beyond the length of the oestrus cycle. Gestation thus extends into the post-luteal and pro-oestrous phases without suppressing follicular growth, so that ovulation occurs within a few days before or after parturition (Tyndale-Biscoe & Renfree 1987). Suckling of the neonate then suppresses full development of the new corpus luteum and the next luteal phase does not appear. If conception occurs post-partum, the embryo is retained as a unilaminar blastocyst in diapause. This condition is termed the quiescent phase, to distinguish it clearly from the other phases of the normal cycle and from anoestrus (Clark & Poole 1967; Sharman & Berger 1969). In the anoestrous state, the ovaries may contain corpora albicantia, but there is no corpus luteum or Graafian follicle, the uteri are very small and the endometrial glands are short and straight with closed lumina (Newsome 1964; Clark & Poole 1967). Quiescence is usually associated with the suckling of a young in the pouch. In the Tammar and Red-necked Wallabies it also persists for several months after weaning (Sharman & Berger 1969). These two species have both a lactational and a seasonal quiescence (Tyndale-Biscoe, Hearn & Renfree 1974).

Conversely, females may enter anoestrus during lactation either annually, as in the Western and Eastern Grey Kangaroos (Poole & Catling 1974), or in response to drought, as in the Red Kangaroo (Newsome 1964). Four conditions, therefore, can be distinguished in macropodid reproductive cycles: lactational and seasonal quiescence and lactational and seasonal anoestrus (Tyndale-Biscoe *et al*. 1974).

The endocrine role of the corpus luteum has been well defined in macropodids, particularly in the Tammar Wallaby (Tyndale-Biscoe 1984; Tyndale-Biscoe & Renfree 1987). Progesterone is the main steroid in corpora lutea of this wallaby (Renfree & Heap 1977; Renfree *et al*. 1984). The progesterone concentration remains at 10–11 ng/mg until day 13 after activation of embryo development by the removal of the pouch young and then rises progressively to a peak of 32 ng mg at day 22 (Renfree, Green & Young 1979). The mass of the single corpus luteum was initially about 10 mg. From day five it enlarges to reach a maximum of about 50–60 mg at day 15–18. It remains large until immediately prior to parturition on day 25. As a result, the total progesterone content is maximal during days 21–23 at about 1.2 μg, rapidly declining to half this on the day of birth, with peripheral plasma concentrations diminishing to quiescent levels shortly thereafter.

The pattern of circulating plasma progesterone is similar in all the species so far studied (Fig. 29.12). During lactational or seasonal quiescence, peripheral plasma concentrations are low, around 100-200 pg/ml, rising to a transient early pulse which occurs at day 3–4 in the Quokka and day 4, 5 or 6 in the Tammar and Red-necked Wallabies (Bradshaw *et al*. 1975; Tyndale-Biscoe & Hinds 1981; Walker & Gemmell 1983a) after reactivation of the diapausing blastocyst. Peak concentrations are reached in late pregnancy (Fig. 29.12) followed by a precipitous fall at the time of parturition. The corpus luteum is the source of this progesterone.

The marsupial corpus luteum does not appear to depend on a luteotrophic stimulus for progesterone secretion nor is activity determined by luteolysins (Hearn 1974; Tyndale- Biscoe & Hawkins 1977; Sernia, Hinds & Tyndale-Biscoe 1980). Direct evidence of pituitary-ovarian interactions is known only for the Tammar Wallaby. FSH and LH, which have been detected in that species (Gallo *et al*. 1978), are not required for luteal reactivation, pregnancy, parturition or lactogenesis, but they are for follicular growth and post- partum oestrous behaviour (Hearn 1972a, 1974; Short *et al*. 1985). Sutherland, Evans & Tyndale-Biscoe (1980) and Tyndale-Biscoe *et al*. (1983) confirmed a low level (0.2–1.9 ng/ml) of LH present at all times except for a pre-ovulatory surge of 10–50 ng/ml in the Tammar Wallaby. This surge is of some 12 hours duration, occurring about 8 hours after oestrus (15 hours post-partum) and 24–40 hours before ovulation.

In intact females, FSH is not detectable (Evans, Tyndale-Biscoe & Sutherland 1980), although it is detectable in intact males (Catling & Sutherland 1980) and reaches very high concentrations (100–600 ng/ml) in castrated males (Catling & Sutherland 1980) and ovariectomised females (Evans *et al*. 1980; Horn, Fletcher & Carpenter 1985) 3–8 days after ovariectomy.

The ovarian cortex of the Tammar Wallaby provides a negative feedback on the pituitary secretion (Tyndale-Biscoe & Hearn 1981) and the corpus luteum presumably also provides a negative feedback during the early phase of the oestrous cycle. Lutectomy during the first 12 days of the cycle leads to premature oestrus and ovulation 9–18 days later (Tyndale-Biscoe & Hawkins 1977), but does not after this day. The corpus luteum thus suppresses the whole of the gonadotrophin-dependent phase during the first half of the cycle, but loses this capacity after day 12. Since progesterone is the major product of the corpus luteum and its output only begins to rise after day 12 coincident with follicular growth, progesterone cannot be responsible for feedback inhibition by the corpus luteum on the pituitary (Tyndale-Biscoe & Renfree 1987). Further, Evans *et al*. (1980) and Renfree, Wallace & Young (1982b) showed that progesterone treatment after lutectomy does not delay premature ovulation or follicular growth, whereas oestradiol does. Similar results were obtained with progesterone in the Quokka (Tyndale-Biscoe 1963b).

The corpus luteum, therefore, holds the central position in the control of reproduction of the Macropodidae (Tyndale-Biscoe & Renfree 1987). The evidence suggests it inhibits follicular development by oestrogens of uncertain origin. By means of progestins, it stimulates the endometrium to secrete specific proteins and polypeptides which probably activate and later support the embryo. As these functions wane, the mature corpus luteum is implicated in the preparation of the genital tract for passage of the foetus at parturition (see below). In this latter function, it may be secreting relaxin as well as progesterone.

Unlike in other marsupials, however, the corpus luteum in macropodids does not provide the sole stimulus to the uterus to maintain gestation. The foeto-placental unit assumes this function during the second half of gestation and, by its influence, determines the length of gestation. There are two semi-independent activities: the ovarian cycle, controlled by the corpus luteum - follicle interaction, and gestation, controlled by the corpus luteum and placenta (Tyndale-Biscoe et al. 1974). The length of the luteal phase, of the follicular phase and of the placental influence determine whether ovulation is prepartum, post-partum or absent among the various species.

Parturition. The present evidence suggests that the control of parturition and the initiation of lactation are similar in marsupials and eutherians. Parturition requires the corpus luteum and both anterior and posterior pituitary be functional, but as in many eutherians, the fetus and placenta also may determine the time of birth in macropodids.

Myometrial activity is relatively quiescent during pregnancy, but at term responds to oxytocin and prostaglandin (Shaw 1983a, 1983b). In the Quokka (Heller 1973), the non-pregnant uterine myometrium is more sensitive to arginine vasopressin than oxytocin. During the luteal phase or pregnancy, the reverse is true and strong contractions of the myometrial smooth muscle is caused by oxytocin, suggesting its possible role in parturition. Parturition occurs via the median vagina and relaxin of luteal origin may be necessary for loosening of the connective tissue of the vagina and urogenital sinus (Tyndale-Biscoe & Renfree 1987). In the Tammar Wallaby, the corpus luteum has an essential role for normal parturition at least up to 21 days after activation of the embryo by removal of the pouch young and for normal development of the mammary gland at least to day 23 after removal of the pouch young (Young & Renfree 1979). Progesterone level is high prior to birth in all species studied (Hinds & Tyndale-Biscoe 1982). Just prior to parturition progesterone falls in the Quokka (Cake, Owen & Bradshaw 1980), the Tammar Wallaby (Hinds & Tyndale- Biscoe 1982; Shaw & Renfree 1984; Lewis, Fletcher & Renfree 1986) and the Red- necked Wallaby (Walker & Gemmell 1983a). Progesterone withdrawal, however, is not essential for parturition (Ward & Renfree 1984).

Oestrogens also are elevated at parturition before the post-partum oestrus (Flint & Renfree 1982; Shaw & Renfree 1984). Parturition can occur in macropodids without a rise in oestrogen since oestrus does not invariably follow parturition in the Tammar Wallaby (M. B. Renfree & I. R. Young unpublished observation). When oestrogen levels are experimentally prevented from rising, females still give birth (Short et al. 1985). In some species, such as the Eastern Grey Kangaroo, oestrus is not common or does not occur post- partum at all, as in the Western Grey Kangaroo. Further, in the Swamp Wallaby, oestrus always occurs prepartum (Tyndale-Biscoe 1984). The Graafian follicle is the main source of oestradiol in the peripheral circulation in the Tammar Wallaby (Harder et al. 1984) and, presumably, in these other species as well.

The sequence of hormonal changes at parturition of the Tammar Wallaby are now clearly defined from recent detailed studies (Flint & Renfree 1982; Shaw 1983a; Tyndale-Biscoe et al. 1983; Harder et al. 1984, 1985; Shaw & Renfree

1984; Ward & Renfree 1984; Lewis *et al*. 1986). Progesterone declines precipitously coincident with, or occasionally within, 6 hours of birth. A sharp rise in oestradiol occurs 8 hours after the progesterone drop and oestrus 10 hours later. The LH surge is dependent on the oestradiol rise and follows it by seven hours. Ovulation follows the LH surge by 24 hours. Oestradiol levels are basal 24 hours after the progesterone fall. There is a transient small pulse of progesterone 16 hours after oestrus and about 8 hours later, which may reflect a switch from oestradiol secretion to progesterone by the granulosa cells (Tyndale-Biscoe & Renfree 1987).

Prostaglandin has been detected in two macropodids: the Tammar Wallaby (Shaw 1983b, Tyndale-Biscoe *et al*. 1983, Lewis *et al*. 1986) and the Red-necked Wallaby, (Walker & Gemmell 1983a). The Tammar Wallaby produces a marked peak of 800–1200 pg/ml of prostaglandin metabolite if collected within 10 minutes of birth. Values decline to less than 200 pg/ml within 45 minutes and are non-detectable by 2 hours post-partum (Lewis *et al*. 1986). Clearly, prostaglandin is elevated during parturition, but the peak is very short-lived.

The foetus of the Tammar Wallaby at parturition has the most obvious effect so far described on the endocrine system. There is a peak of prolactin at parturition which is not observed in nonpregnant females (Tyndale-Biscoe *et al*. 1983). In the Tammar Wallaby, the Agile Wallaby, *M. agilis*, and the Red-necked Wallaby, the interval between one oestrus and the next is shorter and plasma progesterone levels fall more rapidly in females which give birth (Merchant 1979; Merchant & Calaby 1981; Hinds & Tyndale-Biscoe 1982; Tyndale-Biscoe *et al*. 1983). The appearance of elevated prolactin occurs suddenly, about 8 hours before birth and the concentration returns to basal levels by 16 hours post-partum. The prolactin peak precedes the fall in progesterone, the rise in prostaglandin and parturition and precedes the LH peak by 16–28 hours (Tyndale-Biscoe *et al*. 1983; Lewis *et al*. 1986).

Lactation. Marsupials in general, and macropodids in particular, have developed an exquisitely sophisticated lactational physiology. The changing composition of milk has been studied most extensively in macropodids.

Kangaroos and wallabies are able to produce milk of two different kinds from adjacent mammary glands (Griffiths, McIntosh & Leckie 1972; Green 1984) simultaneously. The manner in which this is achieved is not fully understood. Differentiation of the mammary glands begins with each oestrous cycle. Lobulo-alveolar growth is complete at the time of parturition (O'Donoghue 1911; Sharman 1962; Griffiths *et al*. 1972; Findlay 1982). Throughout the course of pregnancy and lactation, the stroma is replaced progressively by alveolar tissue (Findlay 1982). The glands do not reach maximal production of milk until some months after birth. Non-sucked glands regress to a quiescent state. The mechanisms which allow adjacent mammary glands to undergo independent differentiation or de-differentiation are unclear, but local effects induced by sucking are presumed to be important (Findlay & Renfree 1984).

The sucking stimulus and milk withdrawal promote development of the lactating gland. The normal changes in milk composition (see Chapter 17) appear to be an intrinsic characteristic of the glands and occur regardless of the local stimuli produced by the pouch young (Findlay & Renfree 1984). More work has been done on the composition of milk in the Tammar Wallaby than in any other marsupial species (Green 1984). During early pouch life, solids represent only 12% (w/w) of the milk, but there is a gradual increase to 35–40% by the time of weaning (Green, Newgrain & Merchant 1980). Carbohydrates represent a constant 50% of milk solids during the first 26 weeks of pouch life, rising from 7–13 g/100 ml during this period. Between 26–34 weeks postpartum, carbohydrate concentrations decline to 2% of the solids (Messer & Green 1979). Lipids provide 16–19% of the solids up to the end of 26 weeks

(from 2–5 g/100 ml) and then increase rapidly to 23 g/100 ml (to 60% of solids) (Green, Griffiths & Leckie 1983; Green 1984). Proteins remain at 4% for the first 16 weeks, then increase rapidly to 11% at 34 weeks (Green *et al.* 1980; Green & Renfree 1982). Amino acids show marked changes at specific times in the lactation cycle, such as the increase in sulphur-containing amino acids coincident with the appearance of hair follicles at 22 weeks post-partum (Renfree *et al.* 1981b).

As well as structural and compositional changes, there appear to be differing responses to hormones at the various stages of lactation (Tyndale-Biscoe & Renfree 1987). In all mammals, the myoepithelial cells of the mammary gland are sensitive to oxytocin. Exogenous oxytocin causes milk ejection in marsupials. The neurohypophysis of the marsupial contains oxytocin, lysine vasopressin and phenypressin (Ferguson & Heller 1965; Chauvet *et al.* 1983). Macropodid (but not didelphid) oxytocin differs from eutherian oxytocin by a single base sequence change from leucine to isoleucine at position 8, thus making it mesotocin (Ile^8-oxytocin) (Chauvet *et al.* 1981). In the Agile Wallaby, and presumably in other macropodids, the milk ejection response either to injection of exogenous hormone or to electrical stimulation of the presumptive oxytocin neurons in the hypothalamus is similar and shows a greater sensitivity than in eutherians (Lincoln & Renfree 1981a, 1981b). Further, there is a decline in the sensitivity to oxytocin during lactation which allows milk ejection in response to small releases of the hormone to be confined to the gland supporting the small young, whilst both glands would eject milk in response to a sucking episode by the larger young-at-foot. Thus, milk ejection can occur semi-independently in adjacent glands during concurrent asynchronous lactation in response to stimuli produced by a tiny pouch young or a young-at-foot.

Hormone receptor concentrations in the mammary tissue alter during lactation and so may be responsible for this changing sensitivity (Tyndale-Biscoe & Renfree 1987). Prolactin receptor concentrations in the lactating gland of the Tammar Wallaby are known to increase during pregnancy and continue to rise until about 90–100 days of lactation. Receptor concentrations in non-lactating glands decline rapidly after parturition (Stewart & Tyndale-Biscoe 1982; Tyndale-Biscoe, Stewart & Hinds 1984).

Apart from a prepartum pulse of prolactin, concentrations of this hormone in the peripheral circulation remain at less than 40 ng/ml during the first four months of lactation. From 20–24 weeks, it increases and after 24 weeks remains at >100 ng/ml (Hinds & Tyndale- Biscoe 1982). This high concentration is sustained until weaning at around 36 weeks, or until the pouch young is lost. The changeover in prolactin concentration coincides with the greatest changes in the milk composition and in a marked acceleration in the rate of growth of the young.

Seasonal reproduction. Most marsupials are seasonal breeders. Their reproductive cycles are timed so that the young finally vacate the pouch at the most favourable time of the year. Photoperiod appears to be the primary cue in the regulation of this seasonal reproduction, but experiments designed to verify this have been carried out only in three species: the dasyurid Fat-tailed Dunnart, *Sminthopsis crassicaudata* (Godfrey 1969b); the didelphid Virginia Opossum, *Didelphis virginiana* (Farris 1950) and the macropodid Tammar Wallaby *Macropus eugenii* (Hearn 1972b; Sadleir & Tyndale-Biscoe 1977; Hinds & den Ottolander 1983).

The basic macropodid pattern of reproduction is controlled by lactation. It can, however, be affected by environmental conditions in at least two different ways. Firstly, under particularly adverse conditions species such as the Red Kangaroo can become truly anoestrus (Newsome 1964). Secondly, in female Tammar Wallabies the seasonal reproductive pattern is controlled by day length

(Fig. 29.13). Births in the majority of females occur about 1 month after the summer solstice. Pouch emergence is approximately 9 months later, in late spring to early summer. Females come into oestrus, are mated and conceive within 24 hours of giving birth. Consequently, they are normally pregnant for 364 days of the year. The new conceptus grows to a blastocyst of about 100 cells before entering a state of arrested development, or diapause, which lasts for 11 months (Fig. 29.13). As stated above, the sucking activity of the newborn pouch young inhibits luteal development, progesterone secretion and, hence, endometrial activity and blastocyst growth. Removal of the pouch young before the winter solstice allows luteal reactivation and a resumption of embryonic development. This period is therefore referred to as lactational quiescence. If the pouch young is removed after the winter solstice, however, neither the corpus luteum nor the embryo reactivates until the summer solstice. This period is known as seasonal quiescence. Only one other macropodid, the Red-necked Wallaby, is known to display seasonal quiescence (Merchant & Calaby 1981), possibly a relatively recent independent adaptation in each of these two species.

The ovarian activity of the Tammar Wallaby is controlled by a sequence that begins with the frequency of the sucking stimulus to the teat, by a neural arc to the adenohypophysis, presumably via the hypothalamus (Renfree 1979), thence by means of prolactin to suppress development of the corpus luteum. A single dose of the dopamine agonist bromocriptine will induce reactivation of all Tammar Wallaby embryos treated from February to August, but is ineffective in all treated from the vernal equinox in September through to December (Tyndale-Biscoe & Hinds 1984; Tyndale-Biscoe & Renfree 1987). The suppressed corpus luteum, nevertheless, affects FSH and LH secretion by the pituitary so that folliculogenesis and ovulation are inhibited.

Photoperiod stimuli, associated with increasing or long day length, prevent reactivation whereas decreasing or short day length permit reactivation (Sadleir & Tyndale-Biscoe 1977; Hinds & den Ottolander 1983). A constant photoperiod of 15 hours light : 9 hours dark stimulates premature reactivation. The response time after photoperiod change is slower than that seen after removal of pouch young, with the progesterone pulse occurring on day 10 and birth on day 33.

The photoperiodic stimuli are mediated by the pineal gland (McConnell & Tyndale-Biscoe 1985; McConnell 1986; McConnell, Tyndale-Biscoe & Hinds 1986). The release of melatonin, the main pineal hormone, can be prevented by either cutting the sympathetic nerves which supply the pineal (superior cervical ganglionectomy) or by pinealectomy (Renfree *et al*. 1981a; Renfree & Short 1984; McConnell *et al*. 1986). Melatonin injections or implants can terminate embryonic diapause in the Tammar Wallaby and the Red-necked Wallaby (Renfree & Short 1984; Loudon, Curlewis & English 1985; McConnell & Hinds 1985). The pineal is involved, but its precise role is not clear. In some females, corpora lutea reactivate soon after denervation or removal of the pineal, but in other females this does not occur until the normal time after the summer solstice. Either an endogenous circannual rhythm which is independent of the pineal or a residual photosensitivity, the lack of diurnal fluctuations in melatonin notwithstanding, must be invoked to account for such differences (Tyndale-Biscoe & Renfree 1987). These results support the idea that the photoperiodic cue is read as a change in duration of melatonin secreted by the pineal during the dark phase if the period of elevated melatonin is greater than nine hours. Since hypophysectomy during seasonal quiescence is an effective means of inducing immediate reactivation of the corpus luteum, the photoperiod-directed mechanism must ultimately be supposed to operate via the pituitary. As a pulse of prolactin of less than 2 hours duration occurs coincident with the lights coming on in experimental photoperiod pens, prolactin is the most likely agent

A *Macropus eugenii*
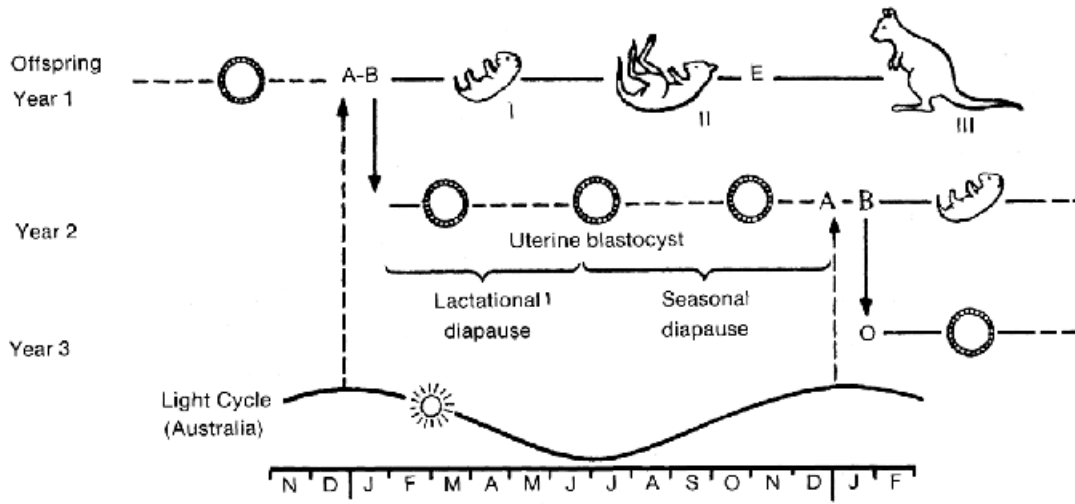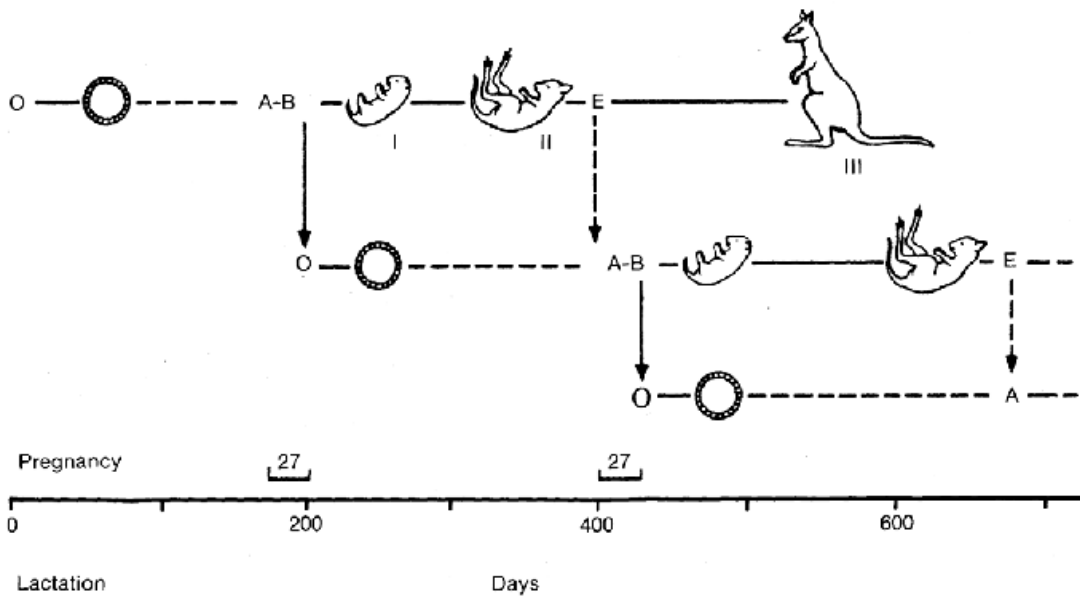

B *Macropus agilis*

Figure 29.13 Patterns of reproduction in: **A**, Tammar Wallaby, a seasonal breeder (gestation 27 days); **B**, Agile Wallaby, a continuous breeder (gestation 27 days). A = activation; B = birth; E = exit from pouch; O = oestrus and ovulation. Dotted arrows indicate activation of blastocyst in diapause; solid arrows post-partum oestrus and ovulation following birth; dotted line periods of diapause of blastocyst; solid line periods of lactation of pouch young. I and II early and late pouch young which suck continuously, III young-at-foot. (After Renfree 1983)

of inhibition (McConnell *et al*. 1986). Melatonin probably does not affect the pituitary directly, but indirectly via a neural mechanism in the hypothalamus (Tyndale-Biscoe & Renfree 1987).

There are few detailed studies of the effects of season on breeding in male macropodids. In two species, the Tammar and the Red-necked Wallaby, in which the reproductive cycles of the females are under precise seasonal control, spermatogenic activity of the testis is unaffected by season and spermatozoa are

produced continuously throughout the year (Catt 1977; Inns 1982). No quantitative studies have been made to determine if the level of sperm production varies during the year. Marked increases in prostate weights were recorded during the main breeding season in both species and a second peak in prostate weight coincided with the time of first oestrus in recently weaned females at a time when adult females were in seasonal quiescence. In Tammar Wallaby males under field conditions, increased prostate weight coincided with seasonal elevation of plasma testosterone levels (Fig. 29.14) (Inns 1982). Catling & Sutherland (1980) clearly demonstrated a stimulatory effect of oestrous females on plasma LH and testosterone levels in males during the breeding season (Fig. 29.14). Reproductive activity of males in these two species, therefore, does not appear to be influenced by photoperiodic changes, but synchronised by behavioural and/or olfactory cues from associated oestrous females.

Although photoperiod has not been shown to influence reproduction in male macropodids, harsh seasonal conditions can affect reproduction by reducing or inhibiting spermatogenic activity of the testis. In Red Kangaroo males, drought-related effects have been shown to impair testicular activity (Newsome 1973).
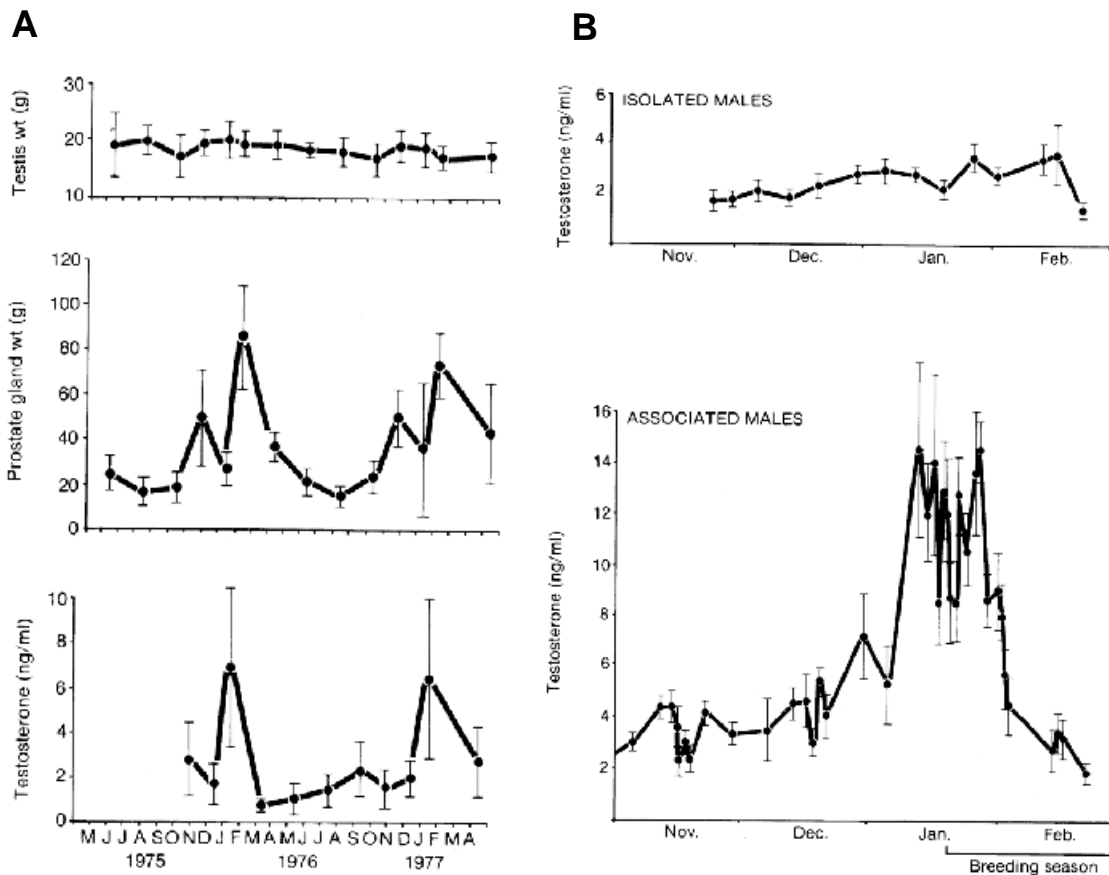

Figure 29.14 Seasonal reproductive activity of Tammar Wallaby: **A**, seasonal changes in testis and prostate weight and in plasma testosterone concentrations of male Tammars in the field during two annual cycles. No seasonal variations are seen in testicular weight, but there is a close correlation between annual peaks in testosterone and prostate weight, which coincide with the breeding season (after Inns 1982); **B**, comparison of plasma testosterone concentrations (mean ±S.E.) in five male tammars isolated from females and eight males associated with females prior to and during the breeding season (After Catling & Sutherland 1980).

Embryology and Development

Embryonic diapause. The processes of ovulation, fertilisation, cleavage and the structure and function of the shell membrane are not greatly different in the Macropodidae from those already described for marsupials in general (Chapter 17). The most characteristic feature of the macropodid conceptus is the phenomenon of embryonic diapause which will be treated in detail here. With the one exception of the Western Grey Kangaroo, all species of the two families of the Macropodoidea investigated exhibit the phenomenon of diapause (Sharman & Berger 1969; Tyndale-Biscoe *et al*. 1974; Renfree 1981). In the control of quiescence and of gestation the Macropodoidea displays a common pattern, distinct from other marsupials and the differences between the species are due to variations in the duration of one or another component. This dynamic interaction provides a control system capable of responding quickly to external factors, such as suckling, drought and photoperiod.

During diapause, blastocyst size varies from 0.25–0.33 mm (Smith 1981) and the diameter of the trophoblast of the species investigated varies from 0.20–0.25 mm (Tyndale-Biscoe 1963a; Renfree & Tyndale-Biscoe 1973a; Tyndale-Biscoe & Renfree 1987). The blastocyst is invariably unilaminar and consists of 70–100 uniform cells in which mitoses are never seen. No part of the trophoblast can be recognised as the presumptive or formative region of the embryo nor can any endoderm mother cells be distinguished.

Blastocysts in diapause are always associated with a quiescent corpus luteum. In the Quokka, the quiescent corpus luteum disappears from the ovary during anoestrus and the blastocyst degenerates (Sharman & Berger 1969; Wallace 1981). In the Tammar Wallaby, however, blastocysts have survived in the uteri for 4 months after bilateral ovariectomy or lutectomy and resumed development when a new corpus luteum or luteinised follicle formed and grew in the remaining ovary (Tyndale-Biscoe & Hearn 1981). In this species, plasma progesterone does not decline after ovariectomy during quiescence (Sernia *et al*. 1980) so that the corpus luteum is not required to maintain diapause. Likewise, the corpus luteum is not required for the embryo to enter diapause (Sharman & Berger 1969). The rate of development up to formation of the unilaminar blastocyst of 80 cells (seventh cleavage division) on day 8 is the same in lactating females with quiescent corpora lutea and in non-lactating females with active corpora lutea (Tyndale-Biscoe & Renfree 1987). By day 10, the blastocysts from non-lactating females are expanded markedly, whereas those from lactating females have entered lactational diapause (Tyndale-Biscoe 1979a; Tyndale-Biscoe & Renfree 1987).

Reactivation after diapause. Once a Tammar Wallaby embryo reaches the unilaminar blastocyst stage (day 8 post-mating), no further development occurs if the female is lactating. The blastocyst apparently awaits a signal from the corpus luteum before development resumes. Reactivation seems to be a three stage process requiring firstly the removal of inhibition from the corpus luteum, secondly a signal from the corpus luteum to the endometrium and thirdly a signal from the endometrium to the blastocyst (Tyndale-Biscoe & Renfree 1987).

The inhibition of the corpus luteum caused by suckling can be stopped by removal of the pouch young. When this is done in the Tammar Wallaby the corpus luteum responds by producing a 2–3 day peak in circulating progesterone and 17β-oestradiol (Hinds & Tyndale-Biscoe 1982; Shaw & Renfree 1984). It seems likely that the progesterone is the effective signal to the endometrium, since physiological levels of progesterone, but not of oestradiol, can reactivate quiescent blastocysts in ovariectomised macropodids (Tyndale- Biscoe 1963b; Clark 1968; Berger & Sharman 1969; M.B. Renfree & A.E. Jetton unpublished data). Four days after removal of the pouch young in Tammar Wallabies, protein

synthesis and secretion by the endometrium increases (Renfree 1972b, Shaw & Renfree 1986). On day 5, RNA activity changes in the blastocyst which has increased in size by day 8 (Renfree & Tyndale-Biscoe 1973a; Moore 1978; Thornber, Renfree & Wallace 1981; Shaw & Renfree 1986). Ovariectomy after day 6 does not prevent the appearance of a luteal uterus and fetal development to full term and it is clear that effective reactivation has occurred by this time.

Evolution of diapause. Two theories have been put forward to account for diapause in macropodid marsupials. Sharman & Berger (1969) considered that it evolved as an adaptation to prevent the birth of a succession of young during the lengthy period of lactation. Tyndale-Biscoe (1968, 1973) addressed a different aspect of the phenomenon and proposed that it is an expression of a fundamental requirement for synchrony between the period of rapid blastocyst expansion and an endometrium capable of providing the means for its accomplishment. The corpus luteum, by its secretion, is the essential gland that coordinates the two. Because the embryos of all marsupials must be dependent on uterine secretion for their early growth and because the corpora lutea stimulate its production, it is possible that diapause at the unilaminar stage is more widespread or even universal among marsupials (for example in the Tarsipedidae, Burramyidae, Dasyuridae) (Tyndale-Biscoe & Renfree 1987).

The macropodid placenta: structure. In all macropodids, the yolk sac blood vessels vascularise part of the chorion. In most, the choriovitelline placenta so formed is the only functional organ of exchange between mother and fetus. The site of attachment is a simple interdigitation between maternal and fetal tissues, where the ectoderm cells have numerous microvilli at their bases (Tyndale-Biscoe 1973). The membrane is probably important in transport and metabolism of uterine secretions, as it has an active appearance both biochemically (Renfree 1973) and ultrastructurally (Tyndale-Biscoe 1973; Tyndale-Biscoe & Renfree 1987).

In the Eastern Grey Kangaroo, the uterus is secretory and the allantois is relatively small and never reaches the chorion (Owen 1834). The well-vascularised yolk sac is in intimate association with the endometrium. The membranes apposed to the uterine wall consist of vascular and non-vascular portions of the yolk sac and only a small area of true chorion, while the allantois remains enclosed in the fold of the yolk sac (Chapman 1882; Owen 1834). Likewise in the Tammar Wallaby, the allantois never reaches the chorion (Fig. 29.15), but urea accumulates in the allantoic fluid, presumably via the patent Wolffian ducts draining the mesonephros (Renfree 1973). A similar arrangement of foetal membranes has been described for the Quokka, the Parma Wallaby, the Red-necked Wallaby and the Common Wallaroo (Caldwell 1884a; Hill 1895, 1901; Sharman 1955b, 1961b; Walker 1983).

There is considerable variation in the degree of invasiveness of the yolk sac placenta and, in most, the shell membrane breaks down on attachment (Hughes 1974; Tyndale-Biscoe *et al*. 1974). Attachment between foetal and maternal cells in the region of the sinus terminalis have been noted in Tammar Wallabies and the potoroid Tasmanian Bettong, *Bettongia gaimardi* (Hughes 1974).

The yolk sac is not attached to the uterine epithelium at any point and no uterine invasion occurs in the Red-necked Wallaby and the Quokka. The uteri are relatively avascular, so that fetal and maternal bloodstreams are well separated (Sharman 1961b).

In most macropodids, the establishment of choriovitelline placentation coincides with the rupture of the shell membrane, when the fetal and maternal blood streams are brought into proximity, as observed in the Tammar Wallaby (Tyndale-Biscoe & Renfree 1987). In the Red-necked Wallaby, the fetal extra-embryonic ectoderm becomes hypertrophied at this time and between day
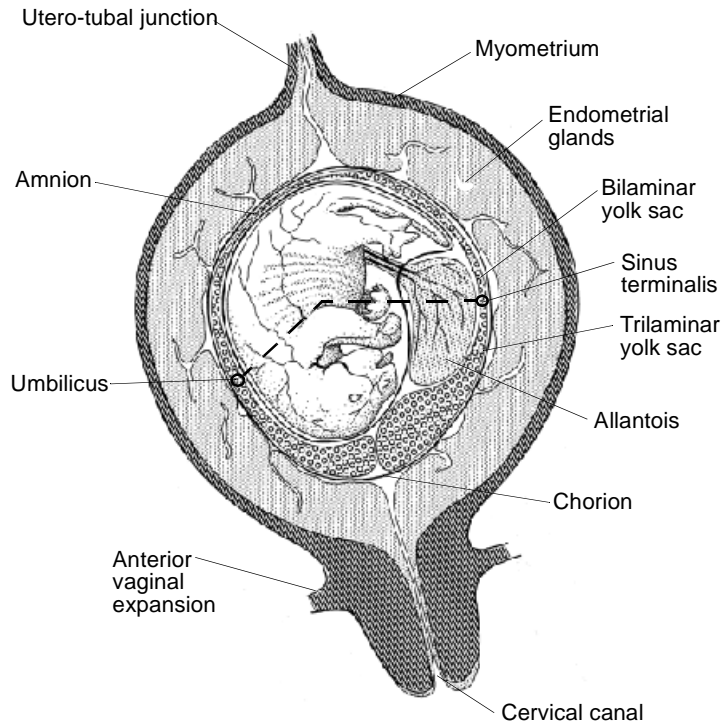
Figure 29.15 Diagrammatic representation of the full term fetus and its membrane within the gravid uterus. The contralateral (non- gravid) uterus is not shown. (© ABRS) [G. Scott]

17–21 is extensively microvillous and active in endocytosis, intracellular transport and synthesis. An extensive subepithelial capillary layer becomes established in the endometrium at this time (Walker 1983).

Placental function. Few biochemical studies of the functions of the placenta have been made. One approach is by analysis of the fetal fluids. During the long free-vesicle or pre- attachment phase, the marsupial blastocyst lies free in the uterine lumen and must gain its nutrients and respiratory requirements by exchanges with the endometrium or luminal fluid. During this time, the composition of the yolk-sac fluid closely resembles uterine fluid.

In the Tammar Wallaby and Quokka, there is a steady increase in the protein content of yolk sac fluid (Renfree 1973; Wallace 1981). The presence of similar proteins in the uterine secretions and in the yolk sac fluid indicates transfer between the two. These molecules, and in particular the pre-albumin group of proteins, may be important for initiation and maintenance of embryonic growth. Their appearance correlates well with other developmental events such as expansion of the blastocyst and onset of RNA polymerase synthesis (Tyndale-Biscoe 1979b; Shaw & Renfree 1986). There is, however, no direct evidence that these proteins derive from the uterine fluids, or that uterine specific proteins are responsible for initiation of growth after diapause or contribute to the brief but rapid pregnancy. Larger proteins in the yolk sac are probably of foetal origin. No detectable [131I]- labelled serum protein injected into pregnant wallabies found its way into the foetus or yolk sac fluid (Renfree 1972b). Transferring blastocysts from adults carrying different genetic polymorphs of the protein transferrin showed that the foetal proteins in the yolk sac fluid were quite unlike either donor or recipient maternal transferrin types (Renfree & Tyndale- Biscoe 1973b).

Concentrations of glucose and urea in yolk sac fluid resemble those in maternal serum, but the concentrations of free amino acids are ten times higher than in serum and three times higher than in uterine fluid, although the protein concentration is much lower than in either (Renfree 1973). After attachment, the composition of the yolk sac fluid is changed noticeably, particularly in its protein components (Renfree 1970), although there are no apparent changes in proteins in serum or endometrial fluid. Glucose and amino acids probably continue to cross the yolk sac from the mother throughout pregnancy. Allantoic and amniotic fluids do not change in glucose or protein concentration. The overall pattern suggests that the yolk sac membrane actively controls the transmission of material across it and the accumulation of substances within the yolk sac fluid. Furthermore, soluble enzymes are found in the yolk sac fluid of both Tammar Wallabies (Renfree 1974) and Virginia Opossums (Renfree & Fox 1975) so that synthesis in the fluid could supplement the foetal nutrient supply.

The various biochemical data support the structural evidence that the two parts of the yolk sac share the functions of respiration and nutrition and that the dramatic change in protein composition of the yolk sac fluid at the time of apposition or attachment reflects the differentiation of the foetal organs and their assumption of the capacity to synthesise proteins.

In Tammar Wallabies, the shell membrane is lost around day 18–19 (Renfree 1973) and in Red-necked Wallabies between day 17–21 (Walker & Rose 1981; Walker 1983). Development is very rapid in all species after it is lost. The theoretical idea that marsupials lack an immune barrier and so have a short gestation period has gained unwarranted popularity (see Lillegraven 1975, 1979, 1985). Walker & Tyndale-Biscoe (1978), however, provided the first experimental evidence, recently amply confirmed by Rodger, Fletcher & Tyndale-Biscoe (1985), that marsupial foetuses must have some immunological barrier.

Few attempts have been made to define the ability and capacity of the marsupial placenta to produce hormones, but Quokkas and Tammar Wallabies do have incipient placental endocrine activity (Bradshaw *et al*. 1975; Renfree & Heap 1977). The yolk sac membrane in the Tammar Wallaby converts a range of steroid precursors into a variety of products, although levels of conversion are generally low (Heap, Renfree & Burton 1980). There is no evidence for the enzymes arylsulphatase or sulphotransferase in the placenta. The yolk sac membrane apparently has enzymes predominantly associated with steroid catabolism and with incipient progesterone synthesis (Heap et al. 1980). By contrast, endometrial and ovarian tissues in Tammar Wallabies have a much greater steroid metabolic capacity (Heap *et al*. 1980; Renfree *et al*. 1984). Although the marsupial yolk sac placenta produces some of the hormones similar to those of eutherians, an important difference is that aromatase activity, pronounced in the sow and the mare (Perry *et al*. 1976; Heap *et al*. 1979), is undetectable in the Tammar Wallaby (Heap *et al*. 1980; Renfree *et al*. 1984). Aromatase, however, is present in ovarian cortex, brain and adrenal tissue (Callard, Petro & Tyndale-Biscoe 1982; Renfree *et al*. 1984).

Marsupial placentae may also have gonadotrophic activity. Preliminary results show that the placental material in the Tammar Wallaby has biological activity (M.B. Renfree & B.M. Hobson unpublished data). Whether this is due to a non-specific effect or a genuine gonadotrophin awaits more specific assay.

Later stages of intrauterine development and organogenesis. The detailed features of the early macropodid conceptus are few. Their general description is given together with those of other species in Chapter 17. Cleaving eggs have been illustrated only for the Tammar Wallaby (Tyndale-Biscoe 1979b; Tyndale-Biscoe & Renfree 1987) and the early bilaminar stages for Tammar Wallabies and Red-necked Wallabies (Tyndale-Biscoe & Renfree 1987). Details of the

post-blastocyst development also are given in Chapter 17. As we have seen above, relatively more is known of the later stages of intrauterine development together with descriptions of the placentation of Macropodidae, but particular details of organogenesis still are limited to those known for the Tammar and the Red-necked Wallaby, with limited observations on other species (Renfree 1972b, 1973; Walker & Rose 1981, Tyndale-Biscoe & Renfree 1987). These are detailed below, with the exception of sex differentiation, which is treated in Chapter 17.

The kidney of the phalangerid Common Brushtail Possum was well studied in the early 1900s (Parker 1917; Buchanan & Fraser 1918; Tribe 1918; Fraser 1919). Later work on Tammar Wallabies (Renfree 1973) and Red-necked Wallabies (Walker & Rose 1981) showed that, as in the possum, the non-functional pronephros appears first, during the free vesicle phase, shortly followed by the differentiation of the mesonephros into distinct tubules, complete with glomeruli and Bowman's capsules. The pronephros is first seen in the 16–17 day Tammar Wallaby embryo (Renfree 1972b) and mesonephric tubules in the 18–19 day Tammar Wallaby and Red-necked Wallaby (Renfree 1972b; Walker & Rose 1981). The Wolffian duct is patent to the allantois and the mesonephric tubules. In the Tammar Wallaby and other macropodids, the proctodaeum is closed (Renfree 1972b) and results in an accumulation of excretory products, notably urea, in the allantoic vesicle (Renfree 1973).

The mesonephros functions as an active excretory organ for the first week after birth (Buchanan & Fraser 1918; McCrady 1938; Bancroft 1973; Krause, Cutts & Leeson 1979; Walker & Rose 1981; Wilkes 1984). Degeneration of the mesonephros in the Tammar Wallaby is first apparent 5 days post-partum (Wilkes 1984).

The neonatal metanephros consists only of a few collecting tubules and a few immature nephrons. Sex is indeterminate at birth and the gonad, which is in proximity to the mesonephros, is at the indifferent stage (Hill & Hill 1955; Renfree 1972b; Bancroft 1973; Alcorn 1975; Walker & Rose 1981).

The lung undergoes early development, with the diaphragm separating the heart and lungs from the peritoneal cavity well before birth. The lung of the neonatal opossum shows peculiarities which make it appear that respiration is carried on in specially modified bronchi and bronchioles before the alveoli and the infundibular portion of the lungs is developed (Selenka 1887; Bremer 1904). More recent studies of *Dasyurus*, *Didelphis*, *Isoodon* species and Red-necked Wallabies confirm this (Hill & Hill 1955; Krause & Leeson 1973; Gemmell & Little 1982; Walker & Gemmell 1983b). As in other mammals, marsupials also may utilise a surfactant as an essential agent in allowing the lungs to be functional at birth, although the mucous secreting cells (the goblet and submucosal cells) are absent (Krause & Leeson 1973; Krause, Cutts & Leeson 1976; Gemmell & Little 1982; Walker & Gemmell 1983b).

The buccal cavity shows structural adaptations that permit permanent attachment to the teat and permit breathing and feeding to proceed simultaneously. The tongue is very large and there is a complex epiglottis.

In the Tammar and Red-necked Wallaby the pancreatic anlagen is present before a recognisable stomach rudiment, but does not enlarge until the liver and stomach are fully differentiated (Renfree 1972b; Walker & Rose 1981). The adrenal also differentiates by day 24 as a discrete group of cells adjacent to the mesonephros. By the day before birth, the cells are organised into cords and appear fully functional. The zonation of the adrenal of the Tammar Wallaby occurs postnatally. A distinct medulla does not appear until day 60 (Call *et al*. 1980), but the presence of cortisol in the foetal plasma indicates cortical

function prior to birth (Catling & Vinson 1976). A similar degree of structural differentiation is evident in the Red-necked Wallaby and the glands contain 0.58 ng of cortisol/adrenal at birth (Walker & Gemmell 1983b).

Rathke's pouch closes off from the pharynx at about day 21 in the Tammar Wallaby embryo and the pituitary is a well-developed, glandular structure by day 24 (Renfree 1972b). Presumptive somatotrophs are found in most regions of the pars distalis (Leatherland & Renfree 1983a). Presumptive mammotrophs, corticotrophs, thyrotrophs and gonadotrophs together represent less than 3% of the pars distalis (Leatherland & Renfree 1983a). The neonatal pituitary also contains vasopressin (Wilkes 1984). The various structural and biochemical observations suggest that the foetal pituitary may function before birth. To know the concentration of hormones in the prenatal pituitary would be of considerable interest.

The macropodid neonate has, like other marsupials, a mixture of precocious and altricial features, sufficiently developed to climb to the pouch, suck and digest milk and excrete waste products, whilst relying on the mother for temperature regulation and the basic provision of growth factors via the milk. At the end of the long development period in the marsupium, however, the newly weaned marsupial is at a similar stage of growth to the weaned eutherian young.

NATURAL HISTORY

Life History

A few macropodid species in southern Australia are strictly seasonal breeders. These include the Quokka, the Tammar Wallaby and the population of Red-necked Wallabies in Tasmania. Many others show a seasonal peak in otherwise year-round breeding. Arid-adapted species may cease breeding for lengthy periods during drought and are able to respond quickly to the return of favourable conditions by coming into oestrus and conceiving.

All macropodid species produce only one young at a birth (like most potoroids). This neonate weighs 0.3–0.9 g, is a few millimetres long and is 'embryonic' by eutherian standards, being the product of a gestation lasting only 27–37 (mean ~32) days. At birth, the young makes its own way from the cloaca to the pouch, which it enters, and attaches to a teat. Length of gestation varies little between species or with size, being a day or two shorter than the oestrous cycle in all except the Swamp Wallaby. Many macropodid species, however, are capable of embryonic diapause (not included in the above figures for length of gestation) and many species typically have a reproductive sequence consisting of vacation of the pouch by one juvenile, birth within a couple of days, a post-partum oestrus, conception and brief development, then diapause of the embryo until the occupying juvenile is within about 4 weeks of permanently vacating the pouch. Embryonic development then recommences.

Typical length of pouch life ranges between 150–320 days and varies greatly between species, with a weak tendency to be longer in the larger species. It can also vary between and within populations of a species, perhaps in response to seasonal or individual conditions (C.N. Johnson & R.I. Stuart-Dick, personal communication). Birth intervals vary with length of pouch life, ranging between 7–12 months. Within a population, birth intervals may be affected by the sex of the present or previous offspring.

There are two patterns of behaviour following permanent emergence of the juvenile from the pouch. In the larger species of kangaroos, the juvenile spends many months getting in and out of the pouch, gradually integrating its social behaviour and activity schedules with those of its mother. When finally denied re-entry to the pouch (just before birth of the next young), it still follows its

mother and, being unweaned, puts its muzzle into the pouch to suck. By contrast, juveniles of many of the small and medium species have only a short period (a few days or weeks) of getting in and out of the pouch and, once permanently out, may be left 'lying out' in cover while the mother goes away to feed. These two modes correspond to the 'lying out' and 'following' behaviour of ungulate young.

Except in extreme drought conditions, young tend to survive pouch life well. Although females of larger species will, when closely pursued, evict pouch young, this is not usually thought to affect survivorship substantially. Robertshaw & Harden (1986), however, suggest that such loss may be important in the population dynamics of Swamp Wallabies exposed to dingo predation. Most juvenile mortality occurs at or after permanent emergence from the pouch, when the juveniles of several species are very vulnerable to predators for example, the Red Kangaroo, (Shepherd 1981) and Eastern Grey Kangaroo (R.I. Stuart-Dick unpublished data). In most species studied, subadult males disperse from, while at least some subadult females remain within or close to, their mother's range. Males may suffer accelerated mortality during dispersal and generally have a higher adult mortality rate than females. The adult sex ratio in populations of medium and large species (but not always in small, homomorphic species) is biased heavily against males (for example Johnson & Bayliss 1981). This is brought about by sex differences in mortality. Sometimes the sex ratio of juveniles in the pouch or at emergence also is biased. The direction of bias may vary regionally in the larger species (Johnson & Jarman 1983), with more male young produced at the climatic extremes of a species' range. In the Eastern Grey Kangaroo, there also is evidence of seasonal bias in production of the sexes (R.I. Stuart- Dick unpublished data).

Females reach maturity usually at 1–1.5 years, but this may be delayed to 2 or even 3 years in the Red Kangaroo in bad seasons (Newsome 1964) or be as early as 6 months in small species. Onset of female maturity is known to be variable in many species, being influenced by resource quality and availability and population density. Physiological maturity in males occurs at 1–4 years of age, but social maturity is delayed in the heteromorphic, medium to large species for a further 1–4 years. Female fecundity is depressed by poverty of resources and high population density, largely through delayed maturity, but also because some females enter anoestrus.

Ecology

The macropodids form the major radiation of terrestrial herbivores in Australia and New Guinea in recent times. The numbers of species of Potoroidae have declined and the Palorchestidae and Diprotodontidae died out between 10 000 and 100 000 years ago. Macropodid species exhibit adaptations of teeth, mouth, gut morphology and physiology which allow them to subsist on diets consisting mainly of leaves of monocotyledonous and dicotyledonous angiosperms. The family has representatives in almost all terrestrial habitats, but individual species are often narrowly restricted to a combination of vegetation types and substrates appropriate to their particular adaptations. Apart from food resources, the provision of appropriate climatic shelter, accessible water and protection from predators characterise the chosen habitat of a species.

Any macropodid species exposed to high radiant heat loads uses shelter of some kind. None regularly dig a burrow or construct a nest as do some of the potoroids, but many of the smallest species (for example, hare-wallabies and nail-tail wallabies) regularly shelter in the daytime in forms or squats, shallow depressions under dense vegetation. Rock-wallabies and wallaroos shelter in interstices of boulder piles, in caves or under rock overhangs. Most other medium and large species in non-forested environments seek the shade of trees

or shrubs at least for a few hours in the middle of hot days. All species will drink, but only a few of the larger species, the Red Kangaroo in particular, do so frequently in hot weather. The arid-adapted macropodids are generally as impressively independent of free water as their ungulate counterparts.

Species also seek shelter from cold winds and rain and avoid frost. Some bask in the sun on cold mornings. Behavioural thermoregulation, through choice of activity, posture and location, is important in the daily activity schedule of most macropodids except those of rainforests.

Most species feed nocturnally and medium and large species extend this activity into early morning and late afternoon. Because of their diurnal need for shelter, which may be unavailable in their feeding habitat, animals often move twice daily between a feeding habitat and shelter, for example, rock-wallabies; pademelons (Johnson 1980b); swamp wallabies (Wyre 1981); and nail-tail wallabies (Lavery & Tierney in Lavery 1985). This is observed most easily where a species that shelters in forest emerges at dusk to feed on adjacent cleared pasture or cropland. For some species, day and night ranges are quite distinct; in others, the two overlap, the animals simply move between different patches within a mosaic of occupied habitats.

Adults of all species that have been studied appropriately are essentially sedentary. They occupy a persistent home-range, rather than being migratory or nomadic. Home ranges vary from a few hectares in the smallest or the forest-dwelling species, such as the Red- necked Pademelon, *Thylogale thetis*, and the Parma Wallaby (K.A. Johnson 1977a) to a few square kilometres (Eastern Grey Kangaroo, Jarman & Taylor 1983). The Red Kangaroo provides the major exception, with Denny (in Lavery 1985) suggesting maximum home-ranges of over 300 km², although Oliver (1986) estimates much smaller ranges. The popular impression that the Red Kangaroo is nomadic results more from local shifts in preferred habitat in response to herbage conditions than to mass movements of populations (Frith & Calaby 1969; Newsome 1965a). Despite the increasing evidence for their general sedentariness, there is evidence (Frith 1964; Frith & Calaby 1969; Denny in Lavery 1985; Oliver 1986) that some Red Kangaroo individuals can move tens or even hundreds of kilometres, but do not do so regularly. Subadults, especially males, range more widely than do established adults.

Studies of feeding have concentrated on the largest species and those of dry or open habitats (Jarman 1984). Nevertheless, casual observations permit description of diets throughout the family. Grasses dominate the diets of the largest species, although the Red Kangaroo also utilises chenopods and other drought-resistant shrubs in dry times. Medium-sized species of the rainforest, such as the Red-legged Pademelon, *Thylogale stigmatica*, and tree-kangaroos, eat leaves (including fallen ones) and fruits of forest trees and shrubs. Some forest wallabies eat grasses when those are available, emerging from the cover of forest at night to do so. Most other small and medium-sized species eat a mixture of grasses, occasionally sedges and leaves of forbs or shrubs. All feed selectively, their relatively fine muzzles and narrow incisor arcades enabling them to pick out individual grass leaves. They all show a general preference for green, readily digestible material and avoid, where possible, highly fibrous and dry plant parts. Although many species will select seed-heads of grasses and some forbs, even the smallest macropodids tend not to dig for storage organs of plants, as the potoroids do. There are occasional reports of small and medium macropodids eating insects or other animal matter. The forepaws may be used in manipulating some foods.

The adults of the larger species are relatively immune to all predators except dingoes. The smaller species and juveniles of the larger ones can be hunted by dingoes, the Thylacine, *Thylacinus cynocephalus*, the Tasmanian Devil,

Sarcophilus harrisii and the introduced Fox, *Vulpes vulpes*, as well as Wedge-tailed Eagles. tree-kangaroos avoid predators by climbing trees; rock-wallabies avoid them by seeking refuge on steep cliffs and in the interstices of boulder piles. Most small and medium-sized species hide in dense cover during the day. The largest species, which do not hide, depend on alertness and, when in groups, respond to the alarm of others. They may then attempt to outrun a predator. The removal of dingoes from many pastoral areas of Australia provides an opportunity to compare population densities of some species in similar habitat with and without a major predator. Dingoes appear to depress the density of larger species such as the Red Kangaroo (Caughley *et al*. 1980).

Macropodids are prone to attack by blood-sucking arthropods (such as tabanids, hippoboscids, ticks and lice) and may be grossly disturbed if any of these is abundant. They also carry a range of nematodes; strongyloids in the stomach are particularly obvious and often very numerous. Grey kangaroos have become infected with liver fluke, *Fasciola hepatica*, but generally, macropodids share few diseases with introduced domestic stock or humans. One exception is *Echinococcus granulosus* (hydatid) cysts; kangaroos and wallabies can carry these, but appear not to take part in a true sylvatic cycle (with dingoes) in the absence of infected domestic stock. Kangaroos can suffer from coccidiosis (especially in captivity) and, both in captivity and in the wild, may suffer from lumpy jaw, an acute bacterial infection of the mandible or maxilla, when feeding on tough or spiky fodder.

The present array of macropodid species is much reduced from that of the late Pleistocene. Many potential competitors, especially all the palorchestids and diprotodontids and the larger vombatids, have become extinct. The remaining native herbivores with which they might compete are the three vombatid species at ground level and some possums and fruit-bats for the tree-kangaroos. The plethora of introduced eutherian herbivores, from rabbits to water buffaloes, has provided new direct or indirect competitors.

Behaviour

Macropodids range from non-social species, most of which are small or live in dense habitat, to gregarious species living in well-organised societies. The degree of gregariousness, measured by typical group size, generally increases with body size, openness of habitat and proportion of grasses in the diet (Kaufmann 1974b; Russell 1984). Gregariousness also correlates to some extent with sexual heteromorphism, suggesting that the larger species, found in larger groups, have mating systems which include the denial of mating opportunities to at least some males (Jarman 1983). Several studies show this to be so. The forms of exclusion of some males vary between species, but nearly all depend on a male hierarchy in which the dominant males, usually the largest, use their dominance to keep other males away from a female in or approaching oestrus. Since male macropodids grow throughout life, the largest males also are usually the oldest. A basic component of the male mating strategy is thus to live long and grow to a large size in order to rise to the top of the local male hierarchy. Another aspect is the detection of potentially oestrous females. Macropodid males do this proximally by olfactory testing, sniffing the cloaca and pouch or testing the female's urine. They also may search widely, checking many females, or wait near resources to which females predictably will come (drinking sites, shelter or concentrations of food). Large Red Kangaroo males may preferentially occupy the habitat preferred by those females which are most likely to enter oestrus (Johnson & Bayliss 1981). In no species is there unequivocal evidence of males holding a persistent harem of females nor a territory that is defended against all other males. Some rock-wallaby males

defend access to a set of refuges permanently used by females. The largest males of many species tend to avoid each other, appearing to partition the area between themselves (for example Johnson 1985).

To reach the top of the local hierarchy, a male must confront other males, defeating them in agonistic displays, most of which display his potential fighting powers or, if those fail, by fighting (Fig. 29.16). The smaller macropodid species fight by grappling with the forepaws while scrabbling at the opponent with the hind feet or by jumping onto or over the opponent and striking out with the hind feet. Such species often roll around on the ground while fighting. By contrast, the larger species remain upright, wrestling with paws on each others' necks, shoulders or forearms or breaking out of that grip to prop on their tails and kick out at the opponent's belly. Full-blooded fights are rare, but can last many minutes, even hours, when they do occur. Younger males of the social species spend much time sparring with males of similar size and in this way establish their hierarchical position.

Figure 29.16 Fighting style of large macropodid species. (© ABRS) [K. Hollis]

Courtship consists of olfactory inspection of the female (described above). A female may repulse a male smaller than herself and may resist inspection by any male if she is not in or approaching oestrus. To get a female to stand still a male may block her path by crouching broadside in front of her. Once her oestrous status is established, the male may attempt to mount, testing her readiness for this by approaching her from behind and putting his paws on her rump. In larger species, he may also paw at or pull her tail. When mounted from behind, the male holds the crouching female with his arms firmly grasping her around the abdomen just in front of the hips. Ejaculation, which follows one or several bouts of pelvic thrusting, may be marked by the male throwing up his head or even lifting the female.

A female may be courted by the largest male that has found her. In the more social species, a male may form a consortship with a female approaching oestrus, staying close to her most of the time, repelling smaller males. He, however, may be driven away by any larger male at any stage up to and including copulation. Oestrous females often move widely and, in the social species, may be followed by a string of males in descending order of size. Such activities serve to advertise her state and she is unlikely to be overlooked by the locally most dominant male who, consequently, gets the majority of matings in the population.

Mother/young behaviour (Fig. 29.17) begins with the female cleaning the pouch, cloaca and intervening fur just before giving birth. The neonate is not assisted into the pouch. While in the pouch attached to a teat, the female interacts little with the juvenile except to lick it; this stimulates defaecation and urination; she eats the urine and faeces. After detachment from the teat and, especially, once it has started to emerge from the pouch occasionally, the juvenile begins to interact directly with its mother. They exchange a small range of soft clucking and grunting calls which serve to maintain contact once the juvenile is mobile outside the pouch. The female controls when the juvenile leaves the pouch, choosing the circumstances to reduce risk of attack by predators and, at first, of confusion among other kangaroos. To this latter end, females of some of the large species (for example, the Eastern Grey Kangaroo) isolate themselves when the young is about to vacate the pouch permanently (R.I. Stuart-Dick unpublished data). At that time the mother accepts the juvenile's attempts to put its muzzle into the pouch to suck, but will not allow it to climb back into the pouch. If such conflict is played out within a group of kangaroos, the juvenile may try to approach other females, be rebuffed and get lost.

Juveniles play with their mothers, jumping at them and wrestling with or biting at their ears and tails. Young males will even begin sparring with their mothers. In the gregarious species, play soon switches to peers of the same sex, with whom the growing juvenile spends progressively more of its time. Nevertheless, juveniles of both sexes spend more time with their mother than with any other kangaroo until weaning. In subadult females, this association may continue in gregarious species. Subadult males tend to disperse out of the maternal range, often wandering widely until becoming established in an adult range.

Although mothers and juveniles will groom each other, mutual grooming is otherwise rare, even in the most gregarious macropodids. Grooming is undertaken with the teeth, forepaws, and second and third toes of the hind feet (the syndactylous toes) which have specially adapted grooming claws. Although some species regularly use lying places which become dusty depressions, rolling in dust is rare. Scent marking, by purposeful placing of dung or urine has not been noted, but rock-wallaby, tree kangaroo and Eastern Grey Kangaroo males certainly rub skin secretions onto prominent objects such as rocks, trees, logs or tussock grasses.
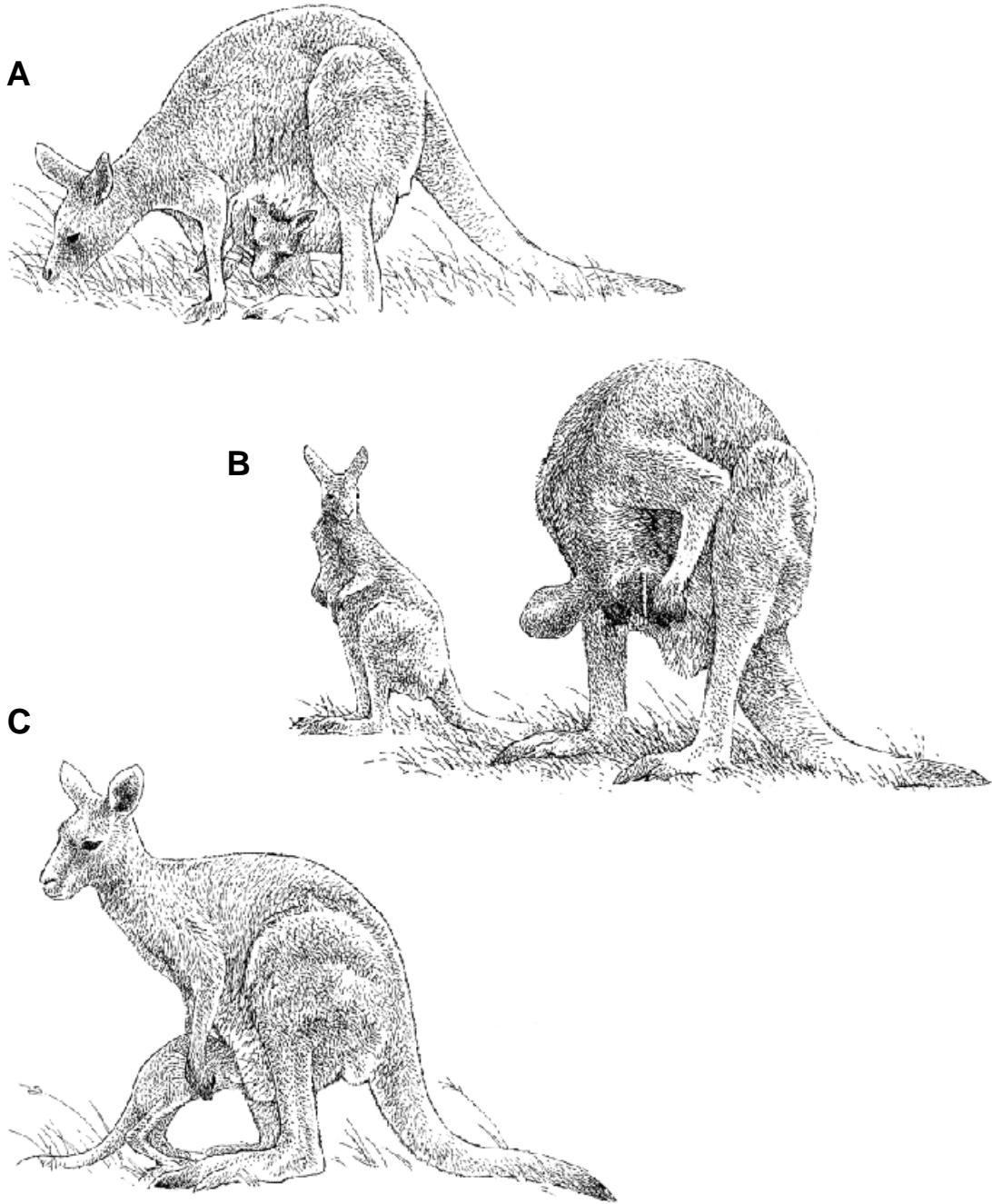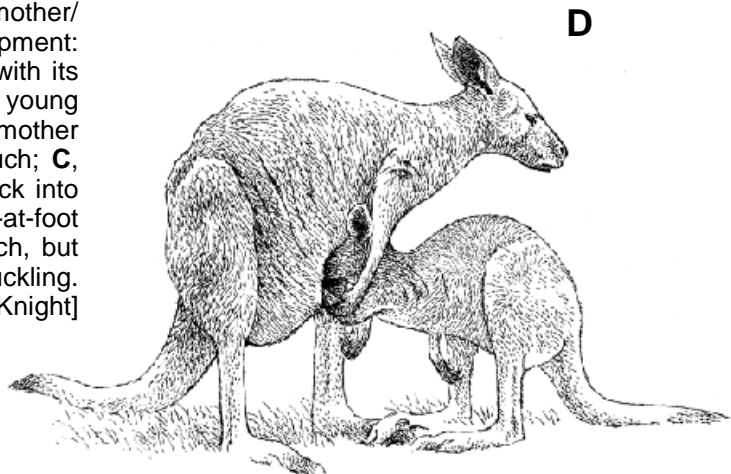
A

B

C

Figure 29.17 Stages of mother/ young behavioural development: **A**, juvenile in the pouch with its head out; **B**, pouch young standing next to the mother while she cleans the pouch; **C**, pouch young climbing back into the pouch; **D**, young-at-foot standing outside the pouch, but with its head in, suckling. (© ABRS)   [F. Knight]

D

Economic Importance

When Europeans invaded Australia, macropodids were the largest terrestrial prey hunted by Aborigines who ate their meat and, in the south-east and Tasmania, used their skins for clothing. Macropodids feature in several phases of Aboriginal art from all parts of the continent. Legends, the locations of sites associated with particular species (along 'dreaming trails') and extant knowledge of practices of habitat manipulation to maintain populations of macropodids point to a profound and sensitive Aboriginal understanding of the resource ecology of these important animals (Newsome 1980, K.A. Johnson, personal communication).

For European settlers, macropodids provided food and skins, but also 'sport'. They were shot, hunted on horse back with or without hounds or driven towards lines of guns or into enclosures where they could be clubbed. To this day macropodids are hunted for 'sport', although on a smaller scale as the practice has declined in acceptability.

Macropodid skins provide furs of moderate quality, used mainly for furry toys and rugs and a fine, soft but strong leather, good for making gloves, shoes, sporting goods and fashion accessories. Since the 1840s, there has been a ready export market for macropodid skins, a trade which now exports only the largest and most abundant species, but which accepted any species a century ago. Skin values in the late 1970s and 1980s have varied from around $4–$6 for an untanned kangaroo skin. In that period, an annual average of about 780 000 skins was exported (Crompton 1983). Macropodids were rarely hunted commercially as food for humans until the mid-20th Century because of the difficulty of delivering field-shot meat to markets in an acceptable condition. Collapse of the export trade in rabbit carcasses in the 1950s myxomatosis epidemic released chillers and refrigerated trucks for storing and transporting kangaroo carcasses. Some of this meat was sold for human consumption, although its export was never sustained because of contamination. Chiller-based shooting, however, then became the basis of a kangaroo industry producing skins and meat used either fresh or canned as pet food.

By the early 1970s, concern for conservation of the larger kangaroos had produced legislation under which only kangaroos that were considered to be locally too numerous could be shot and then only under permit and by the landholder or a licensed 'trapper' or shooter. Shooters supplying meat and skins to the kangaroo industry now provide the major means of controlling the numbers of those large kangaroos that are thought to be damaging pasture, crops, fences or installations. The majority of Australia's estimated 8.3 million red and 10.7 million grey kangaroos (Caughley, Grigg & Short 1983) lives on pastoral or cropping lands. There is little doubt that large numbers of kangaroos could retard cereal crops by grazing their early growth stages, although this does not happen to all crops every year. There is more debate about their impact on pastures. Alternative claims that a kangaroo either eats several times more than a sheep or has no detrimental impact on pasture shared with stock are both exaggerations. Red and grey kangaroos eat ranges of plant species that overlap, but do not precisely coincide with those eaten by stock on the same pasture (for example, Griffiths & Barker 1966). Thus, when pasture growth has ceased or is limiting, kangaroos and stock compete for fodder. Nevertheless, under good conditions kangaroos and stock (especially cattle and horses) select food items so different that direct competition is probably small. The kangaroos' removal of plants not normally eaten by stock may prevent the pasture from becoming dominated by those unpalatable species. Surprisingly, the definitive experiments needed to establish the true costs to pastoralism of stock and kangaroos sharing pasture have never been conducted.

Interactions between kangaroos and agriculture are complex, yet simple solutions to the problems usually have been sought. The industry based on harvesting kangaroos for meat and skins can hold down kangaroo densities regionally, but is not a location-specific remedy. Without it, landholders turn to the next cheapest techniques, some of which (poisoning and drives) are illegal in most States. Fences, especially electric fences, are used increasingly to exclude kangaroos and wallabies from high-value crops. Schemes for integrated control are sometimes proposed (for example Horn 1976).

Macropodids are generally not important reservoirs of pathogens which affect stock or humans. The major exception is their ability to harbour cysticercoid cysts and to be involved, with dingoes, in a sylvatic cycle of this disease (Coman 1972), but this problem exists only where infected sheep also are present.

Macropodids are one of the sights of Australia most eagerly sought by internal and overseas tourists. The medium and large species are easily kept free-ranging in zoos and the large species are fairly easily seen in some national parks. Most small and medium species are difficult to see in the wild. Capture and export of macropodids for public or private collections are strictly controlled, but representative macropodids can be seen in most of the world's major zoos.

In the last 200 years three species of macropodids (the Toolache Wallaby, *Macropus greyi*, *Onychogalea lunata,* and the Eastern Hare-wallaby, *Lagorchestes leporides* have become extinct; the Rufous Hare-Wallaby, *Lagorchestes hirsutus*, the Banded Hare-Wallaby, and The Bridled Nail-tail Wallaby, *Onychogalea fraenata* now occupy less than 5% of their former ranges. These are all small or medium-sized species and are thought to have declined because of habitat alteration. In contrast, some of the largest species appear to have thrived on land modified by European agriculture. While the biology and management of the large species are well understood and practised, the smaller species are not well conserved, although that situation is changing. There are laws controlling the possession, pursuit, taking or killing of all macropodids and their products, but few legal constraints on the destruction of their habitats. Inevitably, the most generalist species, with the most robust resource base, have the best prospects of survival.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The family Macropodidae is ubiquitous in Australia. Members occur throughout most parts of New Guinea and some adjacent islands, including the Aru Islands. Species have been transferred to and established in feral populations in New Zealand, Hawaii, Germany and Britain. There have been few translocations and establishments of feral populations within Australia, although re-establishment of endangered species is being actively researched.

Not all genera were or are equally widely distributed. The hare-wallabies, *Lagorchestes* species, occurred in semi-arid and arid zones of the north and inland; *Lagostrophus* was confined to the semi-arid southwest. Nail-tail wallabies, were found in the tropical north, semi-arid east, southwest and arid centre. Rock-wallabies were found throughout the continent wherever suitably rocky habitats were available. Pademelons were distributed up the mesic, forested east of the continent from Tasmania to New Guinea. Wallabies are similarly confined to the mesic, forested east, but do not occur in Tasmania or New Guinea despite occurring on the mainland immediately across the respective separating straits. The Quokka was confined to the mesic southwest. Tree-kangaroos occur in the forests of eastern Cape York, but the genus is more strongly represented in New Guinea where two more endemic genera of forest-

dwelling macropodids, *Dorcopsis* and *Dorcopsulus*, the only non-Australian genera, are found. The nominate genus, *Macropus*, is ubiquitous, but most species are confined to the continent's mesic fringes. Only the largest species penetrate far into the inland. Only one *Macropus* species, the Agile Wallaby, reaches New Guinea.

Species-richness was greatest in eastern and north-eastern Australia, diminishing towards the inland and south. Tasmania and the south-west were, and are, low in species. The inland, especially the semi-arid zone, was once fairly rich. Now, having lost most of its small and medium species, it is depauperate. The remaining area of greatest species-richness extends from the New South Wales - Queensland border on the eastern fall of the tablelands northwards to central Queensland and up the eastern coast to the base of Cape York. In places in that region, six to eight sympatric macropodids can still be found. In contrast, the Alice Springs region of central Australia now has only two of the five species known to have been there when Europeans arrived. Tasmania retains its only three macropodid species. Off-shore islands, especially those of Western Australia, have given refuge to four species which have become rare or extinct on the mainland, presumably because the islands have not experienced the same detrimental land uses or exotic predators as the mainland.

Affinities with other Groups

The Macropodidae was already distinguishable on dental criteria from its sister family in the Macropodoidea, the Potoroidae, by the Middle Miocene, 15 mybp. In the earliest known macropodid fossils, both families are represented by small (under 2 kg) species, already adapted for hopping (Archer 1984b). Flannery (1984b) suggested that the Macropodoidea shared common pre-Miocene ancestry with the Phalangeridae; these ancestors would have been small, arboreal, leaf and fruit eating inhabitants of the wet forests which covered so much of Australia until the Late Miocene.

While syndactyly and diprotodonty link the macropodoid - phalangeroid lineage to other metatherian herbivore families such as the Phascolarctidae, Vombatidae, Diprotodontidae and Palorchestidae, details of their relationships and times of ancestral separations are unclear. Many arrangements have been proposed, especially for relationships between families within the Diprotodonta. Archer (1984b) attempts to reconcile most modern views with an arrangement which suggests separation of the Diprotodonta into Vombatoidea (Phascolarctidae, Wynyardiidae, Palorchestidae, Diprotodontidae and Thylacoleonidae) and the rest at about 45 mybp. He was undecided about the separation of Macropodoidea from the rest of the phalangeroid stock, giving three alternative derivations: from basal diprotodontan stock at 45 mybp; from basal phalangeroid stock at about 40 mybp; or from a phalangerid - ektopodontid line in the Early Oligocene (35 mybp). Whichever view finally is supported by fossil evidence, the Macropodidae, which Archer (1984b) suggested had split from the Potoroidae by mid-Oligocene, coexisted with the many other families of terrestrial metatherian herbivores for some 30–35 million years before achieving its present position of numerical domination of all other metatherian herbivores, quite suddenly in the last few million years.

Affinities within the Macropodidae

Three subfamilies are recognised within the Macropodidae: the Balbarinae, the Sthenurinae and the Macropodinae. The Balbarinae was a primitive subfamily (possibly including the earliest macropodid fossils from 15 mybp) which disappeared from the fossil record by Late Miocene. The macropodines and sthenurines emerged in Middle to Late Miocene, replacing the balbarines.

Initially, both subfamilies consisted of small species, but each quickly diversified and evolved larger forms (Flannery 1984b). The Sthenurinae differed from Macropodinae in various dental characteristics, including the occlusion of their incisors (sthenurine lower incisors met the upper incisor arcade rather than inserting between them as in most macropodines); most retained large, elongate premolars. The Sthenurinae contained five genera in the Pliocene and these evolved 20 Pleistocene species. *Procoptodon* and *Simosthenurus* had short, broad skulls (Archer 1984b; Flannery 1984b) while *Sthenurus* species had more conventionally elongate heads. These three genera were characterised by monodactylous hind feet (Rich *et al*. 1985), but differed in molar crown height and form and development of lophs and links which indicated specialisation for browsing in some species and grazing in others. All sthenurines, except the diminutive Banded Hare-Wallaby, became extinct at the end of the Pleistocene or early Holocene.

Many more genera of Macropodinae survive and attention has been focused on relationships between living species (Fig. 29.18). The relationships of these to the many extinct Pliocene and Pleistocene species and genera are not always clear. Several extant genera first known from the earliest Pliocene, including *Macropus*, show the early emergence of hypsodonty and presumed adaptation to a diet of grasses in this subfamily. Other genera, however, which are now adapted to life in rainforests (Pademelons and tree-kangaroos) also are known from Early Pliocene deposits. Species adapted to arid regions (nail-tailed wallabies and *Lagorchestes*) are not known until later deposits (Flannery 1984b). The most primitive extant genera are forest-associated and include *Dorcopsis*, *Dorcopsulus* and tree-kangaroos; at least the two most primitive species, *D. inustus* and Lumholtz's Tree-kangaroo, (Groves 1982). Pademelons, *Thylogale*, a slightly more advanced genus of the forest-dwelling small wallabies, and the rock-wallabies, *Petrogale*, appear to be serologically and morphologically closely related (Kirsch 1977a). Speciation within the extant rock-wallabies has been prolific. Serologically, the Quokka seems closer to pademelons and rock-wallabies than to any other genera (Richardson & McDermid 1978). The relationships of the xeric-adapted *Onychogalea* and *Lagorchestes* to other genera are unclear.

Serologically, but not morphologically (based on tooth characters), *Wallabia* lies close to *Macropus* (Kirsch 1977a); indeed, Richardson & McDermid (1978) include it as a subgenus of that genus. *Macropus*, which has the largest extant radiation of mainly grazing macropodids, is divisible, morphologically and serologically, into three extant subgenera and one extinct subgenus (Flannery & Archer 1982). *Macropus (Osphranter)* contains the three extant wallaroo species and the Red Kangaroo; *Macropus (Prionotemnus)* holds the seven smaller 'wallaby' species; and *Macropus (Macropus)* the Eastern and Western Grey Kangaroos (Flannery 1984b). To each would be added some extinct species, especially some giant Pleistocene species in *Macropus* and *Osphranter*. Richardson & McDermid (1978) preferred a fourth extant subgenus, *Macropus (Megaleia)* for the Red Kangaroo.

Fossil Record

The macropodid fossil record is non-existent before the Middle Miocene (15 mybp), when the first balbarine macropodids appear; these were small, hopping species coexistent with primitive potoroids. In Late Miocene deposits (6–8 mybp), balbarine species are absent, but macropodine species appear. At least one species was as large as a modern grey kangaroo (Flannery 1984b). From the Late Miocene there was a rapid radiation of macropodine species. Sthenurine species are known from the earliest Pliocene deposits onwards and the family is abundantly represented in Pliocene and Pleistocene fossil deposits. Pliocene fossils of both subfamilies show the first signs of adaptation to a diet of
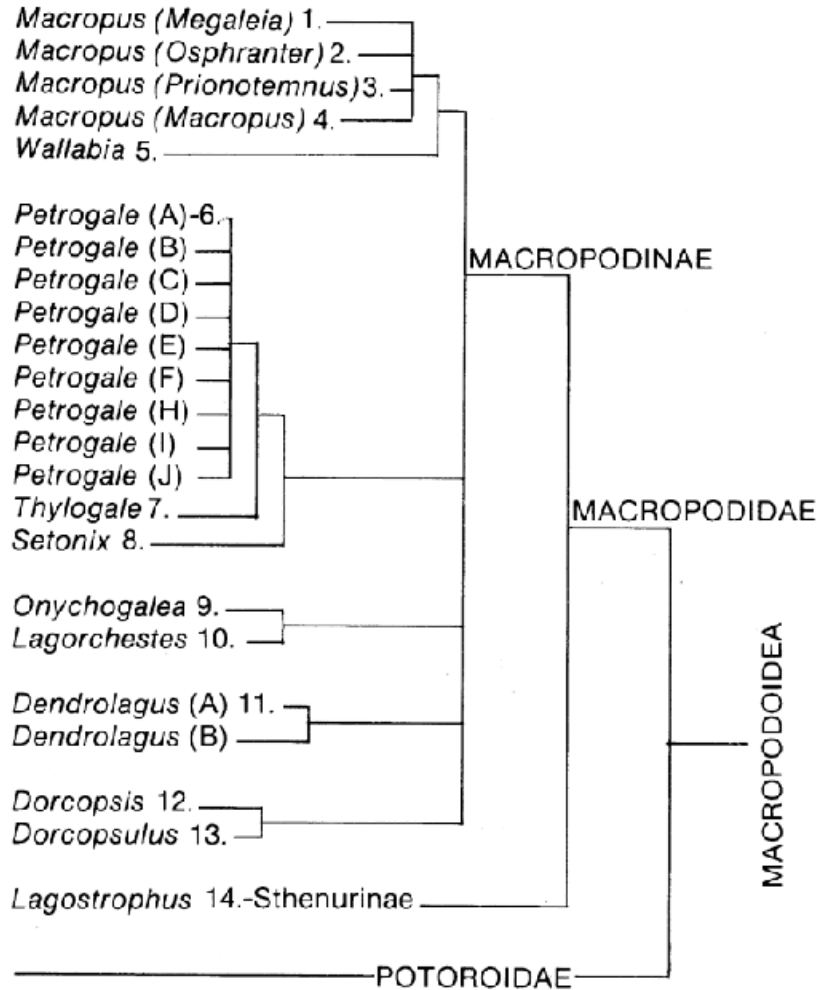
Figure 29.18 Generic relationships within the Macropodidae: 1. contains 1 species, *M. rufus*, formerly a separate genus, recently included (Flannery 1984b) in *Osphranter*; 2. contains *M. robustus*, *M. antilopinus*, and *M. bernardus*, the last said to be the most primitive (Flannery 1984b); 3. may be divisible into two groups, but contains *M. parma*, *M. eugenii*, *M. greyi*, *M. irma*, *M. parryi*, *M. dorsalis*, *M. rufogriseus* and *M. agilis*; 4. contains *M. giganteus* and *M. fuliginosus*; 5. contains *W. bicolor*; 6. *Peradorcas* may be subsumed within *Petrogale*, and the genus splits into 10 groups (Briscoe *et al.* 1982), (a) *P. purpureicollis*, *P. lateralis* and *P. hacketti*, plus unnamed species from the Macdonnell Ranges and western Kimberleys, (b) *P. rothschildi*, (c) *P. inornata*, *P. assimilis*, *P. puella* and two unnamed forms from Queensland, (d) *P. godmani* and an unnamed form from Cape York, (e) *P. penicillata* and *P. herberti*, (f) *P. xanthopus*, (g) *P. persephone*, (h) *P. branchyotis*, (i) *P. burbidgei*, (j) *P. canescens*, P. (formerly *Peradorcas*) *concinna*, and two unnamed forms from Arnhem Land; 7. contains *T. stigmatica*, *T. thetis*, *T. billardierii* and *T. brunii* (the latter confined to PNG); 8. contains only *S. brachyurus*; 9. contains *O. lunata*, *O. fraenata* and *O. ungifera*; 10. contains *L. hirsutus*, *L. conspicillatus*, *L. asomatus* and *L. leporides*; 11. may be divided into two groups, the first (a) containing (Groves 1982) *D. inustus* and *D. lumholtzi*, and the second (b) *D. ursinus*, *D. matschiei* and *D. dorianus*, with *D. bennettianus* being unassigned; 12. contains *D. atrata*, *D. veterum*, *D. luctuosa* and *D. hageni*; 13. contains *D. vanheurni* and *D. macleayi*; 14. contains *L. fasciatus*, the only extant member of the Sthenurinae according to this phylogeny; however, some authorities suggest that many more of the genera of Macropodinae should be included in the Sthenurinae. Indeed, some would leave only *Macropus* and *Wallabia* in the Macropodinae. Sources: Kirsch (1977a); Richardson & McDermid (1978); Rofe (1978); Briscoe *et al.* (1982); Groves (1982); Maynes (1982); Flannery (1983); Archer (1984b); Flannery (1984b).

grasses. Throughout the Pliocene the family displayed consistent trends towards adaptation to aridity, to mobility in open habitats and to increasing size. Many assemblages are species-rich, with up to four or five sympatric species of some genera.

An interesting feature of the Pliocene assemblages is the greater range at that time of genera now confined to rainforest areas of New Guinea or northern Queensland. *Dorcopsis* and *Dendrolagus* species fossils, for example, are found as far south as Victoria and New South Wales. The major evolutionary feature of the Pliocene, however, was the emergence of mesic adaptations in the macropodids, a trend which continued into the Pleistocene. The early Pleistocene faunas contained species which became much less common by late Pleistocene as the more modern macropodid community emerged. Among these early genera were *Bohra*, a giant tree-kangaroo of New South Wales and *Troposodon* which was rapidly replaced in the early Pleistocene by other genera of Sthenurinae. In the Pleistocene, the xeric-adapted genera of macropodines, *Onychogalea* and *Lagorchestes*, first emerged. But the outstanding feature of Pleistocene fossil macropodids is their tendency towards giant size. *Procoptodon*, *Simosthenurus*, *Sthenurus*, *Protemnodon* and *Macropus* all included giant species. All of these giant species became extinct at the end of the Pleistocene. Some of the larger macropodine species which survived the Pleistocene underwent dwarfing, their extant descendants being significantly smaller than the fossils from the late Pleistocene (Flannery 1984b).

The fossil record of the Macropodidae is rich and increasingly well known in late Pliocene and Pleistocene deposits, sufficiently so for changes through time in size and distribution of some common species to be interpretable. The record for the Miocene, however, is fragmentary and does not extend into earlier periods.

COLLECTION AND PRESERVATION

Collection

Several methods have been used to capture wild macropodid marsupials. These vary with the size, behaviour and habitat of the species.

Small wallabies (such as Quokkas, and pademelons) are most effectively caught by enticing them into a permanent enclosure baited with sown improved pasture or pelleted feed. The enclosures used by Johnson (1980b) and Hume (1977) to catch Red-necked Pademelons, measure 20 m^2. Two swing doors in opposite sides of the 2 metre high enclosure are left tied open to allow animals free movement in and out of the enclosure, except during trapping operations. These are carried out by setting the swing doors so that they can be closed by pulling a light line from a position behind a hill or patch of forest approximately 100 m from the enclosure. Any animals caught in the enclosure are quickly herded into a one metre wide laneway along one fence, and confined at the end of this laneway by gates at intervals along the laneway. Some small wallabies may be dazzled with a spotlight and then hand-netted, for example hare-wallabies and nail-tail wallabies.

At least three different methods have been used with rock-wallabies. These are:

(a) Box traps baited with commercial horse pellets and set on known runways. The door must be tied open until the bait is removed regularly by the animals, then set so that it is closed behind when the animal stands on a plate in the centre of the box trap.

(b) Temporary enclosures approximately 5 m in diameter and 1 m high are made from rabbit netting and covered with nylon mesh. Uprights are made from steel posts driven into the soil substratum or supported by a

horizontal foot on rock substrate. The enclosure can be baited with lucerne chaff, commercial horse pellets and, in arid regions, with water. The single swing door is initially tied open, then allowed to swing in both directions once the bait is taken regularly. The size of the door is critical; it must be large enough for rock-wallabies, but too small to admit larger herbivores such as wallaroos, goats and sheep. Doors measuring 300 mm high and 200 mm wide are effective with Yellow-footed Rock-wallabies, *Petrogale xanthopus*, in western Queensland. On the day of trapping, the door is restricted to open inwards only. Any animals caught in the enclosure are removed at dawn, to avoid exposing them to the heat of the sun, by a catcher squeezing through the door while others collapse the trap onto the animals to restrict their movement until grasped by the base of the tail.

(c) Macropod netting of 30–50 mm mesh size is hung in well-used runways in rock clefts. Animals are caught by herding them at dawn from their feeding areas towards their daytime refuge areas amongst the rocks.

Methods that have been used with the larger macropodid marsupials such as large wallabies, wallaroos and kangaroos include:

(a) Constructing permanent yards around watering points such as dams and troughs. Animals can be prevented from leaving by provision of a one-way funnel-shaped entry point. Inside the yard, the animals can be herded into nylon macropod netting (50–100 mm mesh size) suspended from the fence or into a narrow catching laneway.

(b) Macropod netting can be suspended along existing fences and from trees, bushes and steel posts if necessary, to form a wing at an angle of 45–90° to the fence and extending 10–50 m from the fence. Animals are herded along the fence line until they become entangled in the mesh. The net must be set with ample 'belly' and some netting on the ground for maximum effectiveness.

(c) Stunning with a 0.22 long-barrel rifle operated from a vehicle. This is done at night, when some animals can be approached and held in the beam of a spotlight at a distance of less than 100 metres. When standing, the animal can be stunned by shooting just above the skull between the ears. If done correctly the animal will continue standing, disoriented, for up to 30 seconds before moving off. Within this time, catchers must run from the vehicle parallel to but outside the spotlight beam until level with the animal, then quickly tackle it and, by grasping the base of the tail, transfer it into an open-weave hessian bag for transport. Because of the need for swift action across the ground this technique is only suitable in open country with few obstacles such as fallen trees and large rocks.

(d) Immobilisation with a dart containing one or more immobilising or paralysing drugs. Only limited success has been reported with this technique when used on macropodid marsupials and until the technique has been improved it is not recommended for routine use.

(e) Immobilisation with drugs (for example, alphachloralose) administered in food or water.

Post-capture complications

Unless great care is taken with captured wild animals, post-capture losses can be distressingly high. Great care should be taken to minimise stressing the captured animal with exhaustion, fear, drug overdosage or trauma. Macropodid

marsupials seem to be particularly vulnerable to a condition known as capture myopathy. This is, however, just one of the principal causes of post-capture losses (Keep 1976):

1. Capture myopathy;

2. Shock;

3. Hyperthermia and hypothermia;

4. Respiratory failure;

5. Cardiac failure;

6. Trauma (injury);

7. Secondary infections.

Capture myopathy manifests itself from within 12 hours to a month after capture, but usually 1–2 weeks post-capture. It is associated with excessive chasing of animals prior to capture or with their struggling to escape from traps or nets. Affected animals show stiffness and spasms of muscle groups, particularly in the cervical (neck) region. There may be partial paralysis of the limbs, prostration, laboured respiration and increased heart rate. Myoglobinuria may also occur, but in some cases the animal may die from acute heart failure without showing any of the above symptoms.

Shock can occur soon after capture. It is characterised by apathy, prostration, rapid thready pulse, rapid respiration, pale mucous membranes and cold extremities. Shock can result from fear and pain, injury and from immobilising drugs that depress respiration and cause hypotension. It is caused by a fall in either total blood volume (from injury) or effective circulating volume due to vasodilation.

Hyperthermia is a common post-capture complication in conditions of high ambient temperature or humidity and results from excessive chasing, leaving immobilised animals in direct sunlight and from transportation in poorly ventilated vehicles and crates or bags. The symptoms of hyperthermia include panting, sweating, rapid pulse, elevated rectal temperature, coma or convulsions.

Respiratory and cardiac failure are usually associated with overdosage of paralytic of immobilising drugs, particularly in shocked or exhausted animals. Injury to both bony and soft tissues can occur very easily during catching operations, from a variety of causes including falls and collisions during flight, impact with solid trap supports or sides, entanglement in nets, excess momentum of capture projectiles and tying of the limbs of immobilised animals which struggle frantically to escape. Secondary infections of wounds suffered during capture can be largely prevented by systematic administration of broad spectrum antibiotics to any animal at risk.

Techniques for handling macropodid marsupials are described in Fowler (1978).

Maintenance of captive colonies

Most macropodids can be maintained successfully in captivity in outdoor enclosures except in colder climates. In such climates an indoor or a combined indoor-outdoor enclosure is necessary, especially for smaller species. Outdoor enclosures should in any case be provided with shelter from sun, wind and rain (Poole 1982). A source of heating within the shelter would make it possible to maintain the smaller wallabies in outdoor enclosures in all but the coldest climates. Some small species require cover in which to hide during the daylight hours.

The enclosures must be provided with an adequate supply of fresh drinking water; a concrete or galvanised iron trough fitted with a ball valve is probably the best arrangement. Diets used to maintain captive macropodids vary widely among zoos, fauna parks and research institutions. Loose hay (lucerne and grass or meadow hay) or pellets based on chopped (chaffed) hay is the essential dietary item for most macropodids except tree-kangaroos. Good quality hay should provide adequate levels of vitamins A and D without special supplements. A mineral supplement such as a commercial block designed for domestic stock will provide the necessary minerals. Cracked grain (such as wheat) can be provided when energy requirements are elevated as in cold weather. Cracked wheat is also a good source of vitamin E, often found to be deficient in diets fed to captive wallabies. This is because the vitamin E requirement is elevated by any stress associated with captivity. Excessive crowding of wallabies often results in paralysis and incoordination of the hind limbs. This is accompanied by marked wasting of the muscles of the pelvic girdle and the disorder invariably terminates in death. The lesions, however, were completely reversed by oral dosing or intramuscular injection with vitamin E at the rate of 500 mg per day for several days in Quokkas (Kakulas 1961).

Tree-kangaroos can be maintained successfully on a diet of fruit and vegetables (apples, bananas, carrots). Individuals of this genus are folivorous/frugivorous rather than grazers or browsers.

There are two main diseases encountered with captive macropodids. The first is coccidiosis or 'black scours'. Periodic outbreaks of coccidiosis can occur in captive colonies. The condition is characterised by profuse black diarrhoea and in the sub-acute form, death occurs after two or three days. In the acute form, scant, black, often blood-stained diarrhoea occurs, with death ensuing within 24 hours. Medication with amprolium (Amprolmix-plus, Merck, Sharp & Dohme) at 125 ppm of a pelleted diet is effective in preventing the disease (Finnie 1974).

The use of coarse, sharp feeds (such as oat awns) should be avoided for macropodids, since they can cause injury to the mouth. The soft tissues can then be invaded by the bacteria *Fusobacterium necrophorus* and *Corynebacterium pyogenes*. The result can be a cellulitis and necrosis of the tissues of the mouth, particularly the jaw and swelling of the mandibles. This latter symptom is lumpy jaw, the common name for necrobacillosis. Although sharp foods should not be used, the provision of materials for the animals to chew on, such as long dry grass or fibrous bark, especially if the diet is pelleted, will reduce the incidence of lumpy jaw. This is presumably because the oral mucosa is toughened by such materials. The molar teeth must be provided with sufficient work to enable them to be properly shed; grazing macropodid species are notable in exhibiting molar progression, the sequential anterior movement of molars through the dental mill, after which they are lost (Hume 1982).

CLASSIFICATION

Family Macropodidae in Australia

Genus *Lagorchestes* (hare-wallabies) [four species (now two, ed.), two of which are extinct]
Genus *Lagostrophus* (Banded Hare-wallaby (one species)
Genus *Onychogalea* (nail-tail wallabies) (three species, one of which is extinct)
Genus *Petrogale* (rock-wallabies) [eleven species (now 15, ed.)]
Genus *Thylogale* (pademelons) (three species)
Genus *Macropus* (kangaroos, wallaroos and wallabies) [14 species (now 15, ed.), one of which is extinct]
Genus *Setonix* (Quokka) (one species)
Genus *Wallabia* (Swamp Wallaby) (one species)
Genus *Dendrolagus* (tree-kangaroos) (two species)

Note that the above editor's comments are according to CAVS 1999

DESCRIPTION OF THE GENERA

Lagorchestes - Hare-wallabies are small (1.0–4.5 kg), with a head and body of 330–550 mm and tail of 250–490 mm. The hind foot is 120–130 mm long. The head and body are pale brown-grey with lighter underparts. The snout is entirely or partly haired. The tail is moderately haired and tapers.

Lagostrophus - The Banded Hare-wallaby has a weight of 1.3–2.5 kg, with a head and body length of 350–450 mm and tail length of 350–400 mm. The hind foot is 100–120 mm long. The head and body are grizzled grey and the lower back is marked with conspicuous black and white transverse bands. Underparts are grey-white. The fur is very thick. The snout is naked and the tail is evenly haired and tapers.

Onychogalea - Nail-tail wallabies are medium sized (4–9 kg body weight), with a head and body length of 430–700 mm and tail length of 360–700 mm. The hind foot is 120–160 mm long. The head and body are grey to light brown, with lighter underparts. The Bridled Nail-tail Wallaby, *Onychogalea fraenata*, has a distinct white stripe, edged with black, extending from the back of the neck to the armpit on each side of the body. The snout is hairy between the nostrils. The tail tapers and is grey, is slightly crested, with a small, dark horny 'nail' at the tip.

Petrogale - Rock-wallabies are medium-sized wallabies of stocky build. Head and body length ranges from 310–650 mm and the tail from 260–700 mm. The hind foot is 120–170 mm long, with short claws and a thick, granulated pad. The head and body coloration is highly variable among species, in tones of brown, grey and yellow, and may be marked by stripes or patches. Underparts are always lighter. The snout is naked. The tail is long, does not taper and can be barred, crested or plain, but darker towards the tip.

Thylogale - Pademelons are small, compact forest wallabies. Body weights range from 3.5–10 kg, with head and body lengths of 290–630 mm and tail lengths of 270–500 mm. The hind foot is 100–150 mm long. Head and body colour is dark grey to brown, with thick, soft hair. Underparts are lighter in colour. The snout is naked. The tail is short- haired and tapering.

Macropus - This genus contains wallabies 3–4 kg in body weight to kangaroos up to 90 kg. Head and body lengths range from 450–2300 mm and tail lengths range from 350– 1050 mm. Hind foot length is 130–350 mm. All species have a relatively small head, thin forelimbs, long body, enlarged hindquarters and elongated, powerful hind limbs. The head and body can be black, grey, brown or red-brown, with lighter underparts. The snout can be naked to haired. The tail is thick, strong and well haired.

Setonix - The Quokka is a small wallaby (2.7–4.2 kg body weight) with a head and body length of 400–540 mm and a short tail of 250–310 mm. The hind foot is 100–120 mm long. The overall colour is grey-brown with lighter underparts. The snout is naked and the ears are short. The short tail tapers and is close-haired.

Wallabia - The Swamp Wallaby is a large, robust wallaby, 10–20 kg body weight. Head and body length is 670–850 mm and the tail 640–860 mm. The hind foot is 190–210 mm long. The head and body are dark brown to black above and light yellow to strong rufous orange below. The snout is naked and there is a faint grey stripe on the cheek. All four feet are black and the tail is grey at the base, but black along the greater part of its length.

Dendrolagus - Tree-kangaroos are medium to large arboreal animals which move their hind feet independently when climbing in trees. Body weights are 4–13 kg, head and body lengths 480–650 mm, and the tail lengths are with 600–940 mm relatively long, well-haired, cylindrical, untapered and not prehensile. The hind foot is short and broad, 130– 160 mm long, and the forelimbs are almost as long,

unlike other macropodids. The head and body are dark grey or dark brown above, with lighter underparts. The snout is partly haired.

Descriptions of the species of the family Macropodidae can be found in Strahan (1983).

LITERATURE CITED

Alcorn, G.T. (1975). Development of the ovary and urino-genital ducts in the tammar wallaby *Macropus eugenii* (Desmarest 1817). Unpublished PhD Thesis, Macquarie University, North Ryde

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

Bakker, H.R. & Bradshaw, S.D. (1978). Plasma antidiuretichormone levels in tammar wallabies (*Macropus eugenii*) as measured with a toad bioassay. *Journal of Endocrinology* 76: 167-168

Bancroft, B.J. (1973). Embryology of *Schoinobates volans* (Kerr) (Marsupialia: Petauridae). *Australian Journal of Zoology* 21: 33–52

Barker, J.M. (1961). The metabolism of carbohydrate and volatile fatty acids in the marsupial, *Setonix brachyurus*. *Quarterly Journal of Experimental Physiology* 46: 54–68

Bedford, J.M., Rodger, J.C. & Breed, W.G. (1984). Why so many mammalian spermatozoa – a clue from marsupials? *Proceedings of the Royal Society of London B* 221: 221–233

Bentley, P.J. (1955). Some aspects of the water metabolism of an Australian marsupial *Setonix brachyurus*. *Journal of Physiology* 127: 1–10

Bentley, P.J. & Shield, J.W. (1962). Metabolism and kidney function in the pouch young of the macropodid marsupial *Setonix brachyurus*. *Journal of Physiology* 164: 127-137

Berger, P.J. & Sharman, G.B. (1969). Embryonic diapause initiated without the suckling stimulus in the wallaby, *Macropus eugenii*. *Journal of Mammalogy* 50: 630-632

Biggers, J.D. (1966). Reproduction in male marsupials. Pp. 251-280 *in* Rowlands, I.W. (ed.) *Comparative Biology of Reproduction in Mammals*. Symposium of the Zoological Society of London 15. Academic Press : London

Blair-West, J.R. & Gibson, A. (1977). The renin-angiotensin system in marsupials. Pp. 297–306 *in* Schmidt-Nielsen, K., Bolis, N. & Taylor, C.R. (eds.) *Comparative Physiology: Primitive Mammals*. Cambridge University Press : Cambridge

Bourne, G.H. (1949). *The Mammalian Adrenal Gland*. Oxford University Press : London 239 pp.

Bradshaw, S.D., McDonald, I.R., Hahnel, R. & Heller, H.(1975). Synthesis of progesterone by the placenta of a marsupial. *Journal of Endocrinology* 65: 451-452

Bremer, J.L. (1904). On the lung of the opossum. *American Journal of Anatomy* 3: 67-73

Briscoe, D.A., Calaby, J.H., Close, R.L., Maynes, G.M., Murtagh, C.E. & Sharman, G.B. (1982). Isolation, introgression and genetic variation in rock-wallabies. Pp. 73-87 *in* Groves, R.H. & Ride, W.D.L. (eds) *Species at Risk: Research in Australia*. Academy of Science : Canberra

Buchanan, G. & Fraser, E.A. (1918). The development of the urogenital system in the Marsupialia with special reference to *T. vulpecula*. Pt. 1. *Journal of Anatomy* 53: 35–95

Cake, M.H., Owen, F.J. & Bradshaw, S.D. (1980). Difference in concentration of progesterone in the plasma between pregnant and non-pregnant quokkas (*Setonix brachyurus*). *Journal of Endocrinology* 84: 153-158

Calaby, J.H. & Richardson, B.J. (1988). Macropodidae. Pp. 60-80 *in* Walton, D.W. (ed.) *Zoological Catalogue of Australia. Mammalia.* Australian Government Publishing Service : Canberra

Caldwell, W.H. (1884a). On the arrangement of the embryonic membranes in marsupial animals. *Quarterly Journal of Microscopical Science* 24: 655–658

Call, R.N., Catling, P.C. & Janssens, P.A. (1980). Development of the adrenal gland in the tammar wallaby, *Macropus eugenii* Desmarest (Marsupialia : Macropodidae). *Australian Journal of Zoology* 28: 249-259

Callard, G.V., Petro, Z. & Tyndale-Biscoe, C.H. (1982). Aromatase activity in marsupial brain, ovaries and adrenals. *General and Comparative Endocrinology* 46: 541-546

Carrick, F.N. & Cox, R.I. (1973). Testosterone concentrationin the spermatic vein plasma of marsupials. *Journal of Reproduction and Fertility* 32: 338-339

Catling P.C. & Sutherland, R.L. (1980). Effect of gonadectomy, season, and the presence of females on plasma testosterone, luteinizing hormone, and follicle stimulating hormone levels in male tammar wallabies (*Macropus eugenii*). *Journal of Endocrinology* 86: 25-33

Catling, P.C. & Vinson, G.P. (1976). Adrenocortical hormones in the neonate and pouch young of the tammar wallaby, *Macropus eugenii*. *Journal of Endocrinology* 69: 447-448

Catt, D.C. (1977). The breeding biology of Bennett's wallaby (*Macropus rufogriseus fruticus*) in South Canterbury, New Zealand. *New Zealand Journal of Zoology* 4: 401–411

Caughley, G., Grigg, G.C. & Short, J. (1983). How many kangaroos? *Search* 14: 151-152

Caughley, G., Grigg, G.C., Caughley, J. & Hill, G.J.E. (1980). Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* 7: 1-12

Chapman, H.C. (1882). On a foetal kangaroo and its membranes. *Proceedings of the Academy of Natural Sciences Philadelphia* 1881: 468-471

Chauvet, M.T., Colne, T., Hurpet, D., Chauvet, J. & Acher, R. (1983). A multigene family for the vasopressin-like hormones? Identification of mesotocin, lysipressin and phenypressin in Australian macropods. *Biochemical and Biophysical Research Communications* 116: 258-263

Chauvet, M.T., Hurpet, D., Chauvet, J. & Acher, R. (1981). A reptilian neurohypophysial hormone, mesotocin (Ile8- oxytocin) in Australian marsupials. *FEBS Letters* 129: 120-122

Clark, M.J. (1968). Termination of embryonic diapause in the red kangaroo, *Megaleia rufa*, by injection of progesterone or oestrogen. *Journal of Reproduction and Fertility* 15: 347–355

Clark, M.J. & Poole, W.E. (1967). The reproductive system and embryonic diapause in the female grey kangaroo, *Macropus giganteus*. *Australian Journal of Zoology* 15: 441–459

Collett, R. (1884). On some apparently new marsupials from Queensland. *Proceedings of the Zoological Society of London* 1884: 381-388

Coman, B.J. (1972). A sylvatic cycle for the hydatid tapeworm (*Echinococcus granulosus*) in remote areas of eastern Victoria. *Australian Veterinary Journal* 48: 552-553

Cooley, H. & Janssens, P.A. (1977). Metabolic effects of infusion of cortisol and adrenocorticotrophin in the tammar wallaby (*Macropus eugenii* Desmarest). *General and Comparative Endocrinology* 33: 352–358

Crompton, A. (1983). Kangaroo skins - a useful tanning material. 8 pp. *in*, *Kangaroo Management: Proceedings of a Public Forum*, edited by Community Information Service, for National Parks and Wildlife Service, South Australian Department of Environment and Planning

Cummins, J.M. & Woodall, P.F. (1985). On mammalian sperm dimensions. *Journal of Reproduction and Fertility* 75: 153–176

Dawson, T.J. (1977). Kangaroos. *Scientific American* 237(2): 78-89

Dawson, T.J. & Brown, G.D. (1970). A comparison of the insulative and reflective properties of the fur of desert kangaroos. *Comparative Biochemistry and Physiology* 37: 23-38

Dawson, T.J., Robertshaw, D. & Taylor, C.R. (1974). Sweating in the kangaroo: a cooling mechanism during exercise, but not in the heat. *American Journal of Physiology* 227: 494–498

De Vis, C.W. (1887). Notice of a probable new species of *Dendrolagus*. *Proceedings of the Royal Zoological Society of Queensland* 3: 11-14

Disselhorst, R. (1904). Die mannlichen Geschlechtsorgane der Monotremen und einiger Marsupialen. *Denkschriften der Medizinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 6: 122-150

Evans, S.M., Tyndale-Biscoe, C.H. & Sutherland, R.L. (1980). Control of gonadotrophin secretion in the female tammar wallaby (*Macropus eugenii*). *Journal of Endocrinology* 86: 13–24

Farmer, S., Licht, P., Bona Gallo, A., Mercado-Simmen, R.,DeLisle, G.E. & Papkoff, H. (1981). Studies of several marsupial anterior pituitary hormones. *General and Comparative Endocrinology* 43: 336-345

Farris, E.J. (1950). The opossum. Pp. 256-267 *in* Farris E.J. (ed.) *The Care and Breeding of Laboratory Animals*. John Wiley & Sons : New York

Fawcett, D.W., Neaves, W.B. & Flores, M.N. (1973). Comparative observations on intertubular lymphatics and the organization of the interstitial tissue of the mammalian testis. *Biology of Reproduction* 9: 500-532

Ferguson, D.B. & Heller, H. (1965). Distribution of neurohypophyseal hormones in mammals. *Journal of Physiology* 180: 846–863

Findlay, L. (1982). The mammary glands of the tammar wallaby (*Macropus eugenii*) during pregnancy and lactation. *Journal of Reproduction and Fertility* 65: 59–66

Findlay, L. & Renfree, M.B. (1984). Growth, development and secretion of the mammary gland of macropodid marsupials. Pp. 403–432 *in* Peaker, M., Vernon, R.G. & Knight, C.H. (eds) *Physiological Strategies in Lactation*. *Symposia of the Zoological Society of London* 51. Academic Press : London

Finnie, E.P. (1974). Prophylaxis against coccidiosis in kangaroos. *Australian Veterinary Journal* 50: 276

Flannery, T.F. (1983). Revision in the macropodid subfamily Sthenurinae (Marsupialia: Macropodoidea) and the relationships of the species of Troposodon and Lagostrophus. *Australian Mammalogy* 6: 15-28

Flannery, T.F. (1984b). Kangaroos : 15 million years of Australian bounders. Pp. 817-836 *in* Archer, M. & Clayton , G. (eds) *Vertebrate Zoogeography & Evolution in Australasia*. (Animals in Space & Time). Hesperian Press : Carlisle

Flannery, T.F. & Archer, M. (1982). The taxonomy and distribution of (Marsupialia : Macropodidae). *Australian Mammalogy* 5: 261-265

Flint, A.P.F. & Renfree, M.B. (1982). Oestradiol-17ß in the circulation during seasonal reactivation of the diapausing blastocyst in a wild population of tammar wallabies (*Macropus eugenii*). *Journal of Endocrinology* 95: 293-300

Forbes, D.K. & Tribe, D.E. (1969). Salivary glands of kangaroos. *Australian Journal of Zoology* 17: 765–775

Fowler, M.E. (1978). *Restraint and Handling of Wild and Domestic Animals*. Iowa State University Press : Ames

Fraser, E.A. (1919). The development of the urogenital system in the Marsupialia, with special reference to *Trichosurus vulpecula*. Part II. *Journal of Anatomy* 53: 97–129

Frith, H.J. (1964). Mobility of the red kangaroo. *CSIRO Wildlife Research* 9: 1-19

Frith, H.J. & Calaby, J.H. (1969). *Kangaroos*. F.W. Cheshire : Melbourne 209 pp.

Frith, H.J. & Sharman, G.B. (1964). Breeding in wild populations of the red kangaroo, *Megaleia rufa*. *CSIRO Wildlife Research* 9: 86-114

Gallo, A.B., Licht, P., Farmer, S.W., Papkoff, H. & Hawkins, J. (1978). Fractionation and biological actions of pituitary gonadotrophins from a marsupial, the wallaby (*Macropus eugenii*). *Biology of Reproduction* 19: 680–687

Gemmell, R.T. & Little, G.J. (1982). The structure of the lung of the newborn marsupial bandicoot, *Isoodon macrourus*. *Cell and Tissue Research* 223: 445-453

Godfrey, G.K. (1969b). Influence of increased photoperiod on reproduction in the dasyurid marsupial, *Sminthopsis crassicaudata*. *Journal of Mammalogy* 50: 132–133

Green, B. (1984). Composition of milk and energetics of growth in marsupials. Pp. 369–387 *in* Peaker, M., Vernon, R.G. & Knight, C.H. (eds) *Physiological Strategies in Lactation. Symposia of the Zoological Society of London* 51. Academic Press : London

Green, B., Griffiths, M. & Leckie, R.M.C. (1983). Qualitative and quantitative changes in milk fat durinq lactation in the tammar wallaby (*Macropus eugenii*). *Australian Journal of Biological Sciences* 36: 455-461

Green, B., Newgrain, K. & Merchant, J. (1980). Changes in milk composition during lactation in the tammar wallaby (*Macropus eugenii*). *Australian Journal of Biological Sciences* 33: 35–42

Green, L.M.A. (1961). Sweat glands in the skin of the quokka of Western Australia. *Australian Journal of Experimental Biology* 39: 481–486

Green, L.M.A. (1963a). Distribution and comparative histology of cutaneous glands in certain marsupials. *Australian Journal of Zoology* 11: 250–272

Green, S.W. & Renfree, M.B. (1982). Changes in the milk proteins during lactation in the tammar wallaby *Macropus eugenii*. *Australian Journal of Biological Sciences* 35: 145–152

Griffiths, M.E. & Barker, R. (1966). The plants eaten by sheep and by kangaroos grazing together in a paddock in south-western Queensland. *CSIRO Wildlife Research* 11: 145-167

Griffiths, M.E., McIntosh, D.L. & Leckie, R.M.C. (1969b). The effects of cortisone on nitrogen balance and glucose metabolism in diabetic and normal kangaroos, sheep and rabbits. *Journal of Endocrinology* 44: 1–12

Griffiths, M.E., McIntosh, D.L. & Leckie, R.M.C. (1972). The mammary glands of the Red Kangaroo with observations on the fatty acid components of the milk triglycerides. *Journal of Zoology, London* 166: 265–275

Groves, C.P. (1982). The systematics of tree kangaroos (*Dendrolagus*: Marsupialia, Macropodidae). *Australian Mammalogy* 5: 157-186

Harder, J.D., Hinds, L.A., Horn, C.A. & Tyndale-Biscoe, C.H.(1984). Oestradiol in follicular fluid and in utero-ovarian venous and peripheral plasma during parturition and post-partum oestrus in the tammar, *Macropus eugenii*. *Journal of Reproduction and Fertility* 72: 551-558

Harder, J.D., Hinds, L.A., Horn, C.A. & Tyndale-Biscoe, C.H.(1985). Effects of removal in late pregnancy of the corpus luteum, Graafian follicle or ovaries on plasma progesterone, oestradiol, LH, parturition and post-partum oestrus in the tammar, *Macropus eugenii*. *Journal of Reproduction and Fertility* 75: 449-459

Harding, H.R. (1977). Reproduction in male marsupials: a critique, with additional observations on sperm development and structure. Unpublished PhD Thesis, University of New South Wales, Kensington

Harding, H.R., Carrick, F.N. & Shorey, C.D. (1979). Special features of sperm structure and function in marsupials. Pp. 289–303 *in* Fawcett, D.W. & Bedford, J.M. (eds) *The Spermatozoan*. Urban & Schwarzenberg : Baltimore

Hayman, D.L. (1977). Chromosome number – constancy and variation. Pp. 27–48 *in* Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. MacMillan : London

Heap, R.B., Flint, A.P.F., Gadsby, J.E. & Rice, C. (1979). Hormones, the early embryo and the uterine environment. *Journal of Reproduction and Fertility* 55: 267-275

Heap, R.B., Renfree, M.B. & Burton, R.D. (1980). Steroid metabolism in the yolk sac placenta and endometrium of the tammar wallaby, *Macropus eugenii*. *Journal of Endrocrinology* 87: 339-349

Hearn, J.P. (1972a). The Pituitary Gland and Reproduction in the marsupial *Macropus eugenii* (Desmarest). Unpublished PhD Thesis, Australian National University, Canberra

Hearn, J.P. (1972b). Effect of advanced photoperiod on termination of embryonic diapause in the marsupial, *Macropus eugenii* (Macropodidae). *Australian Mammalogy* 1: 40–42

Hearn, J.P. (1975a). The role of the pituitary in the reproduction of the male Tammar wallaby, *Macropus eugenii*. *Journal of Reproduction and Fertility* 42: 399–402

Hearn, J.P. (1977). Pituitary function in marsupial reproduction. Pp. 337–344 *in* Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. MacMillan : London

Heller, H. (1973). Effects of oxytocin and vasopressin during oestrous cycle and pregnancy on the uterus of *Setonix brachyurus*. *Journal of Endocrinology* 58: 657-671

Hill, J.P. (1895). Preliminary note on the occurrence of a placental connection in *Perameles obesula*, and on the foetal membranes of certain macropods. *Proceedings of the Linnean Society of New South Wales* 10: 578–581

Hill, J.P. (1901). Contributions to the embryology of the Marsupialia. II. On a further stage in the placentation of *Perameles*. III. On the foetal membranes of *Macropus parma*. *Quarterly Journal of Microscopical Science* 43: 1-21

Hill, J.P. & Hill, W.C.O. (1955). The growth stages of the pouch-young of the Native Cat (*Dasyurus viverrinus*) together with observations on the anatomy of the newborn young. *Transactions of the Zoological Society of London* 28: 349–452

Hinds, L.A. & den Ottolander, R.C. (1983). Effect of changing photoperiod on peripheral plasma prolactin and progesterone concentrations in the tammar wallaby (*Macropus eugenii*). *Journal of Reproduction and Fertility* 67: 57-63

Hinds, L.A. & Tyndale-Biscoe, C.H. (1982). Plasma progesterone levels in the pregnant and non-pregnant tammar, *Macropus eugenii. Journal of Endocrinology* 93: 99-107

Horn, C.A., Fletcher, T.P. & Carpenter, S. (1985). Effects of oestradiol-17ß on peripheral plasma concentrations of LH and FSH in ovariectomised tammars (*Macropus eugenii). Journal of Reproduction and Fertility* 73: 585-592

Horn, R.R. (1976). Wallaby browsing in eucalypt plantations. Pp. 80-100 *in Agriculture, Forestry and Wildlife: Conflict or Coexistence*. P.J. Jarman : Armidale

Hughes, R.L. (1974). Morphological studies on implantation in marsupials. *Journal of Reproduction and Fertility* 39: 173-186

Hume, I.D. (1977). Maintenance nitrogen requirements of the macropod marsupials *Thyogale thetis*, red-necked pademelon, and *Macropus eugenii*, tammar wallaby. *Australian Journal of Zoology* 25: 407-417

Hume, I.D. (1982). *Digestive Physiology and Nutrition of Marsupials*. Cambridge University Press : Cambridge 256 pp.

Hume, I.D. (1984). Principal features of digestion in kangaroos. *Proceedings of the Nutrition Society of Australia* 9: 76-81

Inns, R.W. (1982). Seasonal changes in the accessory reproductive system and plasma testosterone levels of the male tammar wallaby, *Macropus eugenii*, in the wild. *Journal of Reproduction and Fertility* 66: 675–680

Janssens, P.A. & Hinds, L.A. (1981). Long-term effects of corticosteroid administration in the tammar wallaby, *Macropus eugenii. General and Comparative Endocrinology* 45: 56-60

Jarman, P.J. (1983). Mating system and sexual dimorphism in large, terrestrial mammalian herbivores. *Biological Reviews* 58: 1-36

Jarman, P.J. (1984). The dietary ecology of macropod marsupials. *Proceedings of the Nutrition Society of Australia* 9: 82-87

Jarman, P.J. & Taylor, R.J. (1983). Ranging of eastern grey kangaroos and wallaroos on a New England pastoral property. *Australian Wildlife Research* 10: 33-38

Johnson, C.N. (1985). Ecology, social behaviour and reproductive success in a population of red-necked wallabies. Unpublished PhD Thesis, Armidale : University of New England 211 pp.

Johnson, C.N. & Bayliss, P.G. (1981). Habitat selection by sex, age and reproductive class in the red kangaroo in western New South Wales. *Australian Wildlife Research* 8: 465-474

Johnson, C.N. & Jarman, P.J. (1983). Geographical variation in offspring sex ratios in kangaroos. *Search* 14: 152-154

Johnson, J.I. (1977). Central nervous system of marsupials. Pp. 157–278 *in* Hunsaker, D. (ed.) *The Biology of Marsupials*. Academic Press : New York

Johnson, K.A. (1977a). Ecology and Management of the Red-necked Pademelon, on the Dorrigo Plateau of Northern New South Wales. Unpublished PhD Thesis, Armidale : University of New England 351 pp.

Johnson, K.A. (1980b). Spatial and temporal use of habitat by the red-necked pademelon, *Thylogale thetis* (Marsupialia : Macropodidae). *Australian Wildlife Research* 7: 157-166

Jones, F. Wood (1924). *The Mammals of South Australia*. Part II Government Printer : Adelaide pp. 133-270

Jones, I. Chester (1957). *The Adrenal Cortex*. Cambridge University Press : London 316 pp.

Jones, R.C., Hinds, L.A. & Tyndale-Biscoe, C.H. (1984). Ultrastructure of the epididymis of the tammar wallaby, *Macropus eugenii*, and its relationship to sperm maturation. *Cell and Tissue Research* 237: 525–535

Kakulas, B.A. (1961). Myopathy affecting the Rottnest quokka (*Setonix brachyurus*) reversed by α-tocopherol. *Nature* 191: 402-403

Kaufmann, J.H. (1974b). The ecology and evolution of social organization in the kangaroo family (Macropodidae). *American Zoologist* 14: 51-62

Keep, J.M. (1976). Post-capture complications in wild animals. Pp. 21-28 *in*, Australian Fauna Management and Disease. Refresher Course for Veterinarians No. 29, University of Sydney

Kerr, J.B. & Hedger, M.P. (1983). Spontaneous spermatogenic failure in the marsupial mouse *Antechinus stuartii* Macleay (Dasyuridae : Marsupialia). *Australian Journal of Zoology* 31: 445-466

Kinnear, J.E. & Main, A.R. (1976). The recycling of urea nitrogen by the wild tammar wallaby (*Macropus eugenii*) a "ruminant-like" marsupial. *Comparative Physiology and Biochemistry* 51A: 793-810

Kirkpatrick, T.H. (1978). The development of the dentition of *Macropus giganteus* (Shaw). *Australian Mammalogy* 2: 29-36

Kirsch, J.A.W. (1977a). A comparative serology of the Marsupialia, and a classification of the marsupials. *Australian Journal of Zoology Supplementary Series* 52: 1-152

Kolmer, W. (1918). Zur vergleichenden Histologie, Zytologie und Entwicklungsgeschichte der Säugernebenniere. *Archive für mikroskopische Anatomie* 91: 1-97

Krause, W.J. & Leeson, C.R. (1973). The postnatal development of the respiratory system of the opossum. I. Light and scanning electron microscopy. *American Journal of Anatomy* 137: 337-356

Krause, W.J., Cutts, J.H. & Leeson, C.R. (1976). Type II pulmonary epithelial cells of the newborn opossum lung. *American Journal of Anatomy* 146: 181-188

Krause, W.J., Cutts, J.H. & Leeson, C.R. (1979). Morphological observations on the metanephros in the postnatal opossum *Didelphis virginiana. Journal of Anatomy* 129: 459–477

Lavery, H.J. (ed.) 1985. *The Kangaroo Keepers*. University of Queensland Press : St Lucia 211 pp.

Leatherland, J.F. & Renfree, M.B. (1983a). Structure of the pars distalis of pouch-young tammar wallabies (*Macropus eugenii*). *Cell and Tissue Research* 230: 587-603

Leatherland, J.F. & Renfree, M.B. (1983b). Structure of thepars distalis in the adult tammar wallaby (*Macropus eugenii*). *Cell and Tissue Research* 229: 155-174

Lewis, P.R., Fletcher, T.P. & Renfree, M.B. (1986). Prostaglandin in the peripheral plasma of tammar wallabies during parturition. *Journal of Endocrinology* 111: 103-109

Lillegraven, J.A. (1975). Biological considerations of the marsupial-placental dichotomy. *Evolution* 29: 707–722

Lillegraven, J.A. (1979). Reproduction in Mesozoic mammals. Pp. 259-276 *in* Lillegraven, J.A., Kielan-Jaworowski, Z. & Clemens, W.A. (eds) *Mesozoic Mammals: The First Two-thirds of Mammalian History*. University of California Press : Berkeley

Lillegraven, J.A. (1985). Use of the term "trophoblast" for tissues in therian mammals. *Journal of Morphology* 183: 293–299

Lincoln, D.W. & Renfree, M.B. (1981a). Milk ejection in a marsupial, *Macropus agilis*. *Nature* 289: 504-506

Lincoln, D.W. & Renfree, M.B. (1981b). Mammary gland growth and milk ejection in the agile wallaby *Macropus agilis*, displaying concurrent asynchronous lactation. *Journal of Reproduction and Fertility* 63: 193-203

Lincoln, G.A. (1978). Plasma testosterone profiles in male macropodid marsupials. *Journal of Endocrinology* 77: 347–351

Loudon, A.S.I., Curlewis, J.D. & English, J. (1985). The effect of melatonin on the seasonal embryonic diapause of the Bennett's wallaby (*Macropus rufogriseus rufogriseus*). *Journal of Zoology , London* 206: 35-39

MacKenzie, W.C. & Owen, W.J. (1919b). *The Glandular System in Monotremes and Marsupials: Studies and Observations*. Jenkin, Buxton : Melbourne 71 pp.

Maynes, G.M. (1973). Reproduction in the parma wallaby, *Macropus parma* Waterhouse. *Australian Journal of Zoology* 31: 331–351

Maynes, G.M. (1974). Occurrence and field recognition of *Macropus parma*. *Australian Zoologist* 18: 72-87

Maynes, G.M. (1982). A new species of rock-wallaby, *Petrogale persephone* (Marsupialia: Macropodidae) from Proserpine, central Queensland. *Australian Mammalogy* 5: 47-58

McConnell, S.J. (1986). Seasonal changes in the circadian plasma melatonin profile of the tammar, *Macropus eugenii. Journal of Pineal Research* 3: 119–125

McConnell, S.J. & Hinds, L.A. (1985). Effect of pinealectomy on plasma melatonin, prolactin and progesterone concentrations during seasonal reproductive quiescence in the tammar, *Macropus eugenii. Journal of Reproduction and Fertility* 75: 433–440

McConnell, S.J. & Tyndale-Biscoe, C.H. (1985). Response in peripheral plasma melatonin to photoperiodic change and the effects of exogenous melatonin on seasonal quiescence in the tammar, *Macropus eugenii. Journal of Reproduction and Fertility* 73: 529–538

McConnell, S.J., Tyndale-Biscoe, C.H. & Hinds, L.A. (1986). Change in duration of elevated concentrations of melatonin is the major factor in photoperiod response of the tammar, *Macropus eugenii. Journal of Reproduction and Fertility* 77: 623–632

McCrady, E. (1938). *The Embryology of the Oppossum. American Anatomical Memoirs* No. 16: Wistar Institute of Anatomy and Biology : Philadelphia 233 pp.

McDonald, I.R. (1974). Adrenal insufficiency in the red kangaroo (*Megaleia rufa Desm.*). *Journal of Endocrinology* 62: 689-690

McDonald, I.R. (1977). Adrenocortical functions in marsupials. Pp. 345–377 *in* Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. Macmillan : London

McDonald, I.R. & Bradshaw, S.D. (1981). Resistance to the nitrogen-mobilizing, diabetogenic action of cortisol in a small wallaby (*Setonix brachyurus*). *General and Comparative Endocrinology* 43: 39-41

McDonald, I.R. & Waring, H. (1979). Hormones of marsupials and monotremes. Pp. 873–924 *in* Barrington, E.J.W. (ed.) *Hormones and Evolution*. Academic Press : London Vol. 2

Merchant, J.C. (1976). Breeding biology of the agile wallaby, *Macropus agilis* (Gould) (Marsupialia : Macropodidae), in captivity. *Australian Wildlife Research* 3: 93-103

Merchant, J.C. (1979). The effect of pregnancy on the interval between one oestrus and the next in the tammar wallaby, *Macropus eugenii*. *Journal of Reproduction and Fertility* 56: 459-463

Merchant, J.C. & Calaby, J.H. (1981). Reproductive biology of the red-necked wallaby (*Macropus rufogriseus banksianus*) and Bennett's wallaby (*M. r. rufugriseus*) in captivity. *Journal of Zoology , London* 194: 203-217

Messer, M. & Green, B. (1979). Milk carbohydrates of marsupials. II. Quantitative and qualitative changes in milk carbohydrates during lactation in the tammar wallaby (*Macropus eugenii*). *Australian Journal of Biological Science* 32: 519–531

Moore, G.P.M. (1978). Embryonic diapause in the marsupial *Macropus eugenii*. Stimulation of nuclear RNA polymerase activity in the blastocyst during resumption of development. *Journal of Cellular Physiology* 94: 31-36

Myers, K., Bailey, P.J. & Dudzinski, M.L. (1976). The effects of a severe drought on the morphology of the adrenal glands and other indices of health in the red kangaroo *Megaleia rufa* (Desmarest) in north-western New South Wales. *Australian Journal of Ecology* 1: 289-302

Mykytowycz, R. & Nay, T. (1964). Studies of the cutaneous glands and hair follicles of some species of Macropodidae. *CSIRO Wildlife Research* 9: 200–217

Needham, A.D., Dawson, T.J. & Hales, J.R.S. (1974). Forelimb blood flow and saliva spreading in the thermoregulation of the red kangaroo, *Megaleia rufa*. *Comparative Biochemistry and Physiology* 49A: 555–565

Newsome, A.E. (1964). Anoestrus in the red kangaroo *Megaleia rufa* (Demarest). *Australian Journal of Zoology* 12: 9-17

Newsome, A.E. (1965a). The distribution of red kangaroos about sources of persistent food and water in Central Australia. *Australian Journal of Zoology* 13: 289-299

Newsome, A.E. (1965b). Reproduction in natural populations of the red kangaroo *Megaleia rufa* (Desmarest), in Central Australia. *Australian Journal of Zoology* 13: 735-759

Newsome, A.E. (1973). Cellular degeneration in the testis of red kangaroos during hot weather and drought in Central Australia. *Journal of Reproduction and Fertility Supplement* 19: 191-201

Newsome, A.E. (1980). The eco-mythology of the red kangaroo in central Australia. *Mankind* 12: 327-333

Nicholls, E.M. & Rienits, K.G. (1971). Tryptophan derivativeand pigment in the hair of some Australian marsupials. *International Journal of Biochemistry* 2: 593-603

O'Donoghue, C.H. (1911). The growth changes in the mammary apparatus of *Dasyurus* and the relation of the corpora lutea thereto. *Quarterly Journal of Microscopical Science* 57: 187–234

Oliver, A.J. (1986). Social organisation and dispersal in the red kangaroo. Unpublished PhD Thesis, Perth : Murdoch University (10 Chapters unpaginated)

Ortman, R. & Greisbach, W.E. (1958). The cytology of the pars distalis of the wallaby pituitary. *Australian Journal of Experimental Biology and Medical Science* 36: 609-618

Oudemans, J.T. (1892). Die Accessorischen Geschlechtsdrüsen der Säugetiere. *Natuurkundige Verhandelingen van de Bataafsche Hollandsche Maatschappye der Wetenschappen te Haarlem*, 3 Verg. Deel 5, 2 de Stuk 1-99

Owen, R. (1834). On the generation of the marsupial animals, with a description of the impregnated uterus of the kangaroo. *Philosophical Transactions of the Royal Society* 1834: 333-64

Parker, K.M. (1917). The development of the hypophysis cerebri, preoral gut, and related structures in the Marsupialia. *Journal of Anatomy London* 51: 181–249

Parsons, F.G. (1896). On the anatomy of *Petrogale xanthopus* compared with that of other kangaroos. *Proceedings of the Zoological Society of London* 1896: 683–714

Perry, J.S., Heap, R.B., Burton, R.D. & Gadsby, J.E. (1976). Endocrinology of the blastocyst and its role in the establishment of pregnancy. *Journal of Reproduction and Fertility Supplement* 25: 85-104

Poole, W.E. (1973). A study of breeding in grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest) in central New South Wales. *Australian Journal of Zoology* 21: 183–212

Poole, W.E. (1982). Management of captive Macropodidae. Pp. 91-99 in Evans, D.D. (ed.) *The Management of Australian Mammals in Captivity*. Zoological Parks Board of Victoria : Melbourne

Purves, H.D. & Sirett, N.E. (1959). A study of the hormonecontents of the rostral and caudal zones of the pars anterior of the wallaby pituitary. *Australian Journal of Experimental Biology and Medical Science* 37: 271-278

Reid, I.A. & McDonald, I.R. (1968a). Bilateral adrenalectomyand steroid replacement in the marsupial *Trichosurus vulpecula*. *Comparative Biochemistry and Physiology* 26: 613-625

Renfree, M.B. (1970). Protein, amino acids and glucose in the yolk-sac fluids and maternal blood sera of the tammar wallaby, *Macropus eugenii* (Desmarest). *Journal of Reproduction and Fertility* 22: 483-492

Renfree, M.B. (1972b). Influence of the embryo on the marsupial uterus. *Nature* 240: 475–477

Renfree, M.B. (1973). The composition of fetal fluids of the marsupial *Macropus eugenii*. *Developmental Biology* 33: 62–79

Renfree, M.B. (1974). Yolk sac fluid and yolk sac membraneenzymes in the marsupial, *Macropus eugenii*. *Comparative Biochemistry and Physiology* 49B: 273-279

Renfree, M.B. (1979). Initiation of development of diapausing embryo by mammary denervation during lactation in a marsupial. *Nature* 278: 549-551

Renfree, M.B. (1980b). Endocrine activity in marsupial placentation. Pp. 83-86 *in* Cumming, I.A., Funder, J.W. & Mendelsohn, F.A.O. (eds) *Endocrinology 1980*. Australian Academy of Science : Canberra

Renfree, M.B. (1981). Embryonic diapause in marsupials. *Journal of Reproduction and Fertility Supplement* 29: 67-78

Renfree, M.B. (1983). Marsupial reproduction: the choice between placentation and lactation. Pp. 1–29 *in* Finn, C.A. (ed.) *Oxford Reviews of Reproductive Biology*. Clarendon Press : Oxford Vol. 5

Renfree, M.B. & Fox, D.J. (1975). Pre- and post natal development of lactate and malate dehydrogenases in the marsupial *Didelphis marsupialis virginiana*. *Comparative Biochemistry and Physiology* 5B: 347-350

Renfree, M.B. & Heap, R.B. (1977). Steroid metabolism by the placenta, corpus luteum and endometrium during pregnancy in the marsupial *Macropus eugenii*. *Theriogenology* 8: 164

Renfree, M.B. & Short, R.V. (1984). Seasonal reproduction in marsupials. Pp. 789-792 *in* Labrie, F. & Proulx, (eds) *Proceedings of the 7th International Congress of Endocrinology*. Excerpta Medica International Congress Series. Elsevier Science Publishers : Amsterdam

Renfree, M.B. & Tyndale-Biscoe, C.H. (1973a). Intra-uterine development after diapause in the marsupial *Macropus eugenii*. *Developmental Biology* 32: 28-40

Renfree, M.B. & Tyndale-Biscoe, C.H. (1973b). Transferrinvariation between mother and fetus in the marsupial *Macropus eugenii*. *Journal of Reproduction and Fertility* 32: 113-115

Renfree, M.B., Flint, A.P.F., Green, S.W. & Heap, R.B.(1984). Ovarian steroid metabolism and luteal oestrogens in the corpus luteum of the tammar wallaby. *Journal of Endocrinology* 101: 231-240

Renfree, M.B., Green, S.W. & Young, I.R. (1979). Growth ofthe corpus luteum and its progesterone content during pregnancy in the tammar wallaby, *Macropus eugenii. Journal of Reproduction and Fertility* 57: 131-136

Renfree, M.B., Holt, A.B., Green, S.W., Carr, J.P. & Cheek,D.B. (1982a). Ontogeny of the brain in a marsupial (*Macropus eugenii*) throughout pouch life: 1. Brain growth. *Brain, Behaviour and Evolution* 20: 57-71

Renfree, M.B., Lincoln, D.W., Almeida, O.F.X. & Short, R.V.(1981a). Abolition of seasonal embryonic diapause in a wallaby by pineal denervation. *Nature* 293: 138-139

Renfree, M.B., Meier, P., Teng, C. & Battaglia, F.C.(1981b). Relationship between amino acid intake and accretion in a marsupial *Macropus eugenii*. *Biology of the Neonate* 40: 29-37

Renfree, M.B., Wallace, G.I. & Young, I.R. (1982b). Effects of progesterone, oestradiol-17β and and rostenedione on follicular growth after removal of the corpus luteum during lactational and seasonal quiescence in the tammar wallaby. *Journal of Endocrinology* 92: 397-403

Rich, P.V., van Tets, G.F. & Knight, F. (1985). *Kadimakara: Extinct Vertebrates of Australia*. Pioneer Design Studio : Lilydale 248 pp.

Richardson, B.J. & McDermid, E.M. (1978). A comparison of genetic relationships within the Macropodidae as determined from allozyme, cytological and immunological data. *Australian Mammalogy* 2: 43–51

Robertshaw, J.D. & Harden, R.H. (1986). The ecology of the dingo in north-eastern New South Wales. IV. Prey selection by dingoes, and its effect on the major prey species the swamp wallaby *Wallabia bicolor* (Desmarest). *Australian Wildlife Research* 13: 141-163

Rodger, J.C. (1978). Male reproduction - its usefulness in discussion of Macropodidae evolution. *Australian Mammalogy* 2: 73-80

Rodger, J.C. & Hughes, R.L. (1973). Studies of the accessory glands of male marsupials. *Australian Journal of Zoology* 21: 303–320

Rodger, J.C. & White, I.G. (1974b). Free N-acetylglucosamine in marsupial semen. *Journal of Reproduction and Fertility* 39: 383–386

Rodger, J.C., Fletcher, T.P. & Tyndale-Biscoe, C.H. (1985). Active anti-paternal immunization does not affect the success of marsupial pregnancy. *Journal of Reproductive Immunology* 8: 249-256

Rofe, R.H. (1978). G-banded chromosomes and the evolution of the Macropodidae. *Australian Mammalogy* 2: 53-63

Russell, E.M. (1984). Social behaviour and social organization of marsupials. *Mammal Review* 14: 101–154

Russell, E.M. (1985). The Metatherians - Order Marsupialia. Pp.45–104 *in* Brown, R.E. & Macdonald, D.W. (eds) *Social Odours in Mammals*. Oxford University Press : Oxford

Sadleir, R.M.F.S. & Tyndale-Biscoe, C.H. (1977). Photoperiod and the termination of embryonic diapause in the marsupial *Macropus eugenii*. *Biology of Reproduction* 16: 605-608

Sanson, G.D. (1978). The evolution and significance of mastication in the Macropodidae. *Australian Mammalogy* 2: 23-28

Sapsford, C.S., Rae, C.A. & Cleland, K.W. (1969a). Ultrastructural studies on maturing spermatids and on Sertoli cells in the bandicoot *Perameles nasuta* Geoffroy (Marsupialia). *Australian Journal of Zoology* 17: 195–292

Scoggins, B.A., Blair-West, J.R., Coghlan, J.P., Denton, D.A., Myers, D.A., Myers, K., Nelson, J.F., Orchard, E. & Wright, R.D. (1970). The physiological and morphological response of mammals to changes in their sodium status. Pp. 577-602 *in* Benson, G.K. & Phillips, J.G. (eds) *Hormones and the Environment*. Cambridge University Press : London

Selenka, E. (1887). *Studien über Entwickelungsgeschichte der Thiere*. 4. Das opossum, *Didelphis virginiana*. C.W. Kreidel : Wiesbaden 172 pp.

Sernia, C., Hinds, L. & Tyndale-Biscoe, C.H. (1980). Progesterone metabolism during embryonic diapause in the tammar wallaby, *Macropus eugenii*. *Journal of Reproduction and Fertility* 60: 139-147

Setchell, B.P. (1970). Fluid secretion by the testes of an Australian marsupial *Macropus eugenii*. *Comparative Biochemistry and Physiology* 36: 411–414

Setchell, B.P. (1977). Reproduction in male marsupials. Pp. 411–457 *in* Stonehouse, B. & Gilmore, D. (eds) *The Biology of Marsupials*. Macmillan : London

Setchell, B.P. & Carrick, F.N. (1973). Spermatogenesis in some Australian marsupials. *Australian Journal of Zoology* 21: 491–499

Setchell, B.P. & Waites, G.M.H. (1969). Pulse attenuation and countercurrent heat exchange in the internal spermatic artery of some Australian marsupials. *Journal of Reproduction and Fertility* 20: 165–169

Setchell, P.J. (1974b). The development of the thermoregulation and thyroid function in the marsupial *Macropus eugenii* (Desmarest). *Comparative Biochemistry and Physiology* 47A: 1115–1121

Sharman, G.B. (1955b). Studies on marsupial reproduction. III. Normal and delayed pregnancy in *Setonix brachyurus*. *Australian Journal of Zoology* 3: 56-70

Sharman, G.B. (1961b). The embryonic membranes and placentation in five genera of diprotodont marsupials. *Proceedings of the Zoological Society of London* 137: 197–220

Sharman, G.B. (1962). The initiation and maintenance oflactation in the marsupial, *Trichosurus vulpecula*. *Journal of Endocrinology* 25: 375-385 [26]

Sharman, G.B. & Berger, P.J. (1969). Embryonic diapause in marsupials. *Advances in Reproductive Physiology* 4: 211–240

Shaw, G. (1983a). Effect of PGF2α on uterine activity, and concentrations of 13, 14-dihydro-15-keto-PGF2α in peripheral plasma during parturition in the tammar wallaby (*Macropus eugenii*). *Journal of Reproduction and Fertility* 69: 429-436

Shaw, G. (1983b). Pregnancy after diapause in the tammarwallaby, *Macropus eugenii*. Unpublished PhD Thesis, Murdoch University : Perth 179 pp.

Shaw, G. & Renfree, M.B. (1984). Concentrations of oestradiol-17β in plasma and corpora lutea throughout pregnancy in the tammar, *Macropus eugenii*. *Journal of Reproduction and Fertility* 72: 29-37

Shaw, G. & Renfree, M.B. (1986). Uterine and embryonic metabolism after diapause in the tammar wallaby, *Macropus eugenii*. *Journal of Reproduction and Fertility* 76: 339-347

Shepherd, N.C. (1981). Predation of red kangaroos, *Macropus rufus*, by the dingo *Canis familiaris dingo* (Blumenbach), in northwestern New South Wales. *Australian Wildlife Research* 8: 255-262

Short, R.V., Flint, A.P.F. & Renfree, M.B. (1985). Influence of passive immunization against GnRH on pregnancy and parturition in the tammar wallaby, *Macropus eugenii*. *Journal of Reproduction and Fertility* 75: 567–575

Simpson, P.A. & Blair-West, J.R. (1971). Renin levels inthe kangaroo, the wombat and other marsupial species. *Journal of Endocrinology* 51: 79-90

Smith, M.J. (1981). Morphological observations on the diapausing blastocyst of some macropodid marsupials. *Journal of Reproduction and Fertility* 61: 141-150

Stewart, F. & Tyndale-Biscoe, C.H. (1982). Prolactin and luteinizing hormone receptors in marsupial corpora lutea: relationship to control of luteal function. *Journal of Endocrinology* 92: 63-72

Stewart, F., Sutherland, R.L. & Tyndale-Biscoe, C.H. (1981). Macropodid marsupial testicular gonadotrophin receptors and their use in assays for marsupial gonadotrophins. *Journal of Endocrinology* 89: 213-223

Strahan, R. (ed). (1983). *The Australian Museum Complete Book of Australian Mammals*. The National Photographic Index of Australian Wildlife. Angus & Robertson : Sydney xx 530 pp.

Sutherland, R.L., Evans, S.M. & Tyndale-Biscoe, C.H. (1980). Macropodid marsupial luteinising hormone: validation of assay procedures and changes in plasma levels during the oestrous cycle in the female tammar wallaby (*Macropus eugenii*). *Journal of Endocrinology* 86: 1-12

Temple-Smith, P.D. (1984). Reproductive structures and strategies in male possums and gliders. Pp. 89–106 *in* Smith, A.P. & Hume, I.D. (eds) *Possums and Gliders*. Surrey Beatty & Sons with Australian Mammal Society : Sydney

Temple-Smith, P.D. (1984b). Phagocytosis of sperm cytoplasmic droplets by a specialized region in the epididymis of the brush-tailed possum, *Trichosurus vulpecula*. *Biology of Reproduction* 30: 707–720

Thomas, O. (1888). Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum of Natural History. British Museum : London xii 401 pp.

Thornber, E.J., Renfree, M.B. & Wallace, G.I. (1981). Biochemical studies of intrauterine components of the tammar wallaby *Macropus eugenii* during pregnancy. *Journal of Embryology and Experimental Morphology* 62: 325-338

Towers, P., Shaw, G. & Renfree, M.B. (1986). Urogenital vasculature and local steroid concentrations in the uterine branch of the ovarian vein of the female tammar wallaby (*Macropus eugenii*). *Journal of Reproduction and Fertility* 78: 37-47

Tribe, M. (1918). The development of the pancreas, the pancreatic and hepatic ducts in *Trichosurus vulpecula*. *Philosophical Transactions of the Royal Society of London B* 208: 307–350

Tyndale-Biscoe, C.H. (1963a). The role of the corpus luteum in the delayed implantation in marsupials. Pp. 15–32 *in* Enders, A.C. (ed.) *Delayed Implantation*. University of Chicago Press : Chicago

Tyndale-Biscoe, C.H. (1963b). Effects of ovariectomy in the marsupial, *Setonix brachyurus*. *Journal of Reproduction and Fertility* 6: 25–40

Tyndale-Biscoe, C.H. (1968). Reproduction and post-natal development in the marsupial *Bettongia lesueur* (Quoy & Gaimard). *Australian Journal of Zoology* 16: 577–602

Tyndale-Biscoe, C.H. (1973). *Life of Marsupials*. Edward Arnold : London viii 254 pp

Tyndale-Biscoe, C.H. (1979b). Hormonal control of embryonic diapause and reactivation in the tammar wallaby. Pp. 173–190 *in* Whelan, J. (ed.) *Maternal Recognition of Pregnancy*. Ciba Foundation Symposium 64 (new series) Excerpta Medica : Amsterdam

Tyndale-Biscoe, C.H. (1984a). Mammals - Marsupials. Pp. 386-454 *in* Lamming, G.E. (ed.) *Marshall's Physiology of Reproduction*. Vol. 1. Churchill Livingstone : Edinburgh 14th edn

Tyndale-Biscoe, C.H. & Evans, S.M. (1980). Pituitary-ovarian interactions in marsupials. Pp. 259–268 *in* Schmidt-Nielsen, K., Bolis, N. & Taylor, C.R. (eds) *Comparative Physiology: Primitive Mammals*. Cambridge University Press : Cambridge

Tyndale-Biscoe, C.H. & Hawkins, J. (1977). The corpora lutea of marsupials, aspects of function and control. Pp. 245-252 *in* Calaby, J.H. & Tyndale-Biscoe, C.H. (eds) *Reproduction and Evolution*. Australian Academy of Science : Canberra

Tyndale-Biscoe, C.H. & Hearn, J.P. (1981). Pituitary and ovarian factors associated with seasonal quiescence of the tammar wallaby *Macropus eugenii*. *Journal of Reproduction and Fertility* 63: 225-230

Tyndale-Biscoe, C.H. & Hinds, L.A. (1981). Hormonal control of the corpus luteum and embryonic diapause in macropodid marsupials. *Journal of Reproduction and Fertility Supplement* 29: 111-117

Tyndale-Biscoe, C.H. & Hinds, L.A. (1984). Seasonal patterns of circulating progesterone and prolactin and response to bromocriptine in the female tammar, *Macropus eugenii*. *General and Comparative Endocrinology* 53: 58-68

Tyndale-Biscoe, C.H. & Renfree, M.B. (1987). *Reproductive Physiology of Marsupials*. Cambridge University Press : Cambridge 476 pp.

Tyndale-Biscoe, C.H., Hearn, J.P. & Renfree, M.B. (1974). Control of reproduction in macropodid marsupials. *Journal of Endocrinology* 63: 589–614

Tyndale-Biscoe, C.H., Hinds, L.A., Horn, C.A. & Jenkin, G. (1983). Hormonal changes at oestrus, parturition and post- partum oestrus in the tammar wallaby (*Macropus eugenii*). *Journal of Endocrinology* 96: 155-161

Tyndale-Biscoe, C.H., Stewart, F. & Hinds, L.A. (1984). Some factors in the initiation and control of lactation in the tammar wallaby. Pp. 389–401 *in* Peaker, M., Vernon, R.G. & Knight, C.H. (eds) *Physiological Strategies in Lactation*. *Symposia of the Zoological Society of London* 51. Academic Press : London

Van Soest, P.J. (1965). Symposium on factors influencing the voluntary intake by ruminants: Voluntary intake in relation to chemical compostion and digestibility. *Journal of Animal Science* 24: 834-843

Walker, K.Z. & Tyndale-Biscoe, C.H. (1978). Immunological aspects of gestation in the tammar wallaby, *Macropus eugenii*. *Australian Journal of Biological Sciences* 31: 173-182

Walker, M.T. (1983). Gestational hormones: embryonic maintenance in the marsupial *Macropus rufogriseus*. Unpublished PhD Thesis, University of Queensland : St Lucia 243 pp.

Walker, M.T. & Gemmell, R.T. (1983a). Plasma concentrationsof progesterone, oestradiol-17β and 13, 14-dihydro-15-oxo- prostaglandin F2α in the pregnant wallaby (*Macropus rufogriseus rufogriseus*). *Journal of Endocrinology* 97: 369-377

Walker, M.T. & Gemmell, R.T. (1983b). Organogenesis of the pituitary, adrenal, and lung at birth in the wallaby, *Macropus rufogriseus*. *American Journal of Anatomy* 168: 331-344

Walker, M.T. & Rose, R. (1981). Prenatal development after diapause in the marsupial *Macropus rufogriseus*. *Australian Journal of Zoology* 29: 167–187

Wallace, G.I. (1981). Uterine factors and delayed implantation in macropodid marsupials. *Journal of Reproduction and Fertility Supplement* 29: 173–181

Ward, K.L. & Renfree, M.B. (1984). Effects of progesterone on parturition in the tammar, *Macropus eugenii*. *Journal of Reproduction and Fertility* 72: 21-28

White, A.W. & Harrop, C.J.F. (1975). The islets of Langerhans of the pancreas of macropodid marsupials: a comparison with eutherian species. *Australian Journal of Zoology* 23: 309–319

Wilkes, G.E. (1984). The development of structure and function of the kidney in the tammar wallaby, *Macropus eugenii*. Unpublished PhD Thesis, Australian National University : Canberra 204 + 16 pp.

Windsor, D.E. & Dagg, A.I. (1971). The gaits of the Macropodinae (Marsupialia). *Journal of Zoology , London* 163: 165-175

Wyre, G. (1981). Aspects of the activity and behaviour of the swamp wallaby *Wallabia bicolor* (Desmarest) at Hillgrove, New South Wales. Unpublished Honours Thesis, University of New England : Armidale 95 pp.

Young, I.R. & Renfree, M.B. (1979). The effects of corpus luteum removal during gestation on parturition in the tammar wallaby *Macropus eugenii*. *Journal of Reproduction and Fertility* 56: 249-254