FAUNA
of
AUSTRALIA

17. MORPHOLOGY AND PHYSIOLOGY OF THE METATHERIA

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EXTERNAL CHARACTERISTICS

The Metatheria, comprising a single order, Marsupialia, is a large and diverse group of animals and exhibits a considerable range of variation in external features. The variation found is intimately related to the animals' habits and, in most instances, parallels that are found in the Eutheria. Useful general references to external characteristics include Pocock (1921), Jones (1923a, 1924), Grassé (1955), Frith & Calaby (1969), Ride (1970) and Strahan (1983).

Body form

In size, the marsupials range upwards from the Long-tailed Planigale, *Planigale ingrami*, a small, mouse-like animal weighing only around 4.2 g, with a head-body length of 59 mm and a tail 55 mm long. At the other extreme, there are large kangaroos, such as the Red Kangaroo, *Macropus rufus*, in which the males may weigh as much as 85 kg and attain a head-body length of 1400 mm and a tail of 1000 mm.

Body shape also varies greatly. The primarily carnivorous marsupials, the dasyurids (for example, antechinuses, dunnarts, quolls, planigales and others), are small to medium sized quadrupeds with subequal limbs. The tail is relatively slender and generally about half the length of the body. The omnivorous peramelids show increased development of the hind limbs in keeping with their rapid bounding locomotion. Saltatory or hopping forms (for example kangaroos and wallabies), carry the hind limb specialisation to an extreme, with a concomitant reduction of the forelimbs (Fig. 17.1); their tails are thick, muscular, supporting and balancing structures. The climbing forms include the possums with subequal limbs and prehensile tails, the tail-less koalas and the tree-kangaroos of the genus *Dendrolagus*. The latter retain the elongated hind limb of the terrestrial forms but possess strong curved claws and an extremely long tail. The gliding possums have extensive lateral skinfolds, supported by both the fore- and hind limbs when gliding, and a medium to long tail. Fossorial marsupials include the medium sized, solidly built Common Wombat, *Vombatus ursinus,* and the small, highly specialised marsupial moles, *Notoryctes*, notable for its horny nose plate, enlarged claws on digits III and IV of the manus and its naked stubby tail.

Pelage

The fur is generally thick and soft though some taxa, such as *Isoodon* (bandicoots) have bristle-like guard hairs. The colours brown, fawn and grey predominate on the dorsal surface, whilst the ventral surface may be cream or white. Variations in pattern include the paler, dorsal stripes found in the Numbat, *Myrmecobius fasciatus,* and the white spots of some dasyurids. Characteristic mammalian tactile hairs (vibrissae) are found on the face and usually on the carpus; tarsal vibrissae occur in *Petaurus* (gliders) and Brushtail Possums (possums). *Notoryctes* totally lacks such tactile hairs.

Face

The snout may be relatively short as in the *Phalanger* (Cuscus) and wombats or long as in bandicoots (*Perameles*) or the Numbat. The nocturnal forms have large eyes and, frequently, well-developed external ears. The marsupial moles are blind and lack external ears.

Manus and Pes

Each limb extremity usually bears five digits (pentadactyly). Claws and thickened epidermal pads are developed on both manus and pes. Syndactyly is found in the macropodids (kangaroos and wallabies), phalangers and bandicoots and involves reduction in size of pedal digits II and III, which are enveloped in a common skin covering, except for the claws. Digit I may be lost on the foot in the macropodids and also in some dasyurids. Digit IV is greatly increased in size in the saltatorsial macropodids (Fig. 17.2). The *Dactylopsila trivirgata* (Striped Possum) manus has a greatly elongated and attenuated digit IV for extracting insects.

Skin glands

Sternal glands are found on the chest in the Numbat, the antechinuses, the brushtail possums (*Trichosurus*) and the Koala, *Phascolarctos cinereus,* and are more strongly developed in males. More information on these and other skin glands is included in the following section on exocrine glands.

Marsupium and Mammae

Most female marsupials develop a functional pouch which opens anteriorly, but in the bandicoots, marsupial moles and the wombats the opening is posterior. Exceptions to this condition are the vestigial pouch in some small dasyurids such as in dunnarts (*Sminthopsis*) and total absence of the pouch in *Marmosa*, *Caenolestes* (South American opossums), the Numbat and the phascogales (*Phascogale*). The number of mammae is variable and ranges in number from 12 in some dasyurids down to two in wombats, marsupial moles, and the Koala.

External genitalia

There is a single urogenital opening. In males the scrotum is anterior to the urogenital opening within which the penis is normally retracted. In *Notoryctes* the scrotum is absent and the testes are abdominal.

SKELETAL SYSTEM

The bones and the arrangement of bones in the marsupial skeleton essentially follow the basic mammalian pattern (Fig. 17.1). In response to the varied locomotory and feeding habits, the marsupials show many similar adaptations to those found in eutherian mammals, the placentals, but also others that are unique. In addition, there is a series of skeletal features which in combination are unique to, and hence characterise, the Metatheria.

The almost universal presence of epipubic bones distinguishes the marsupial pelvic girdle from that of the Eutheria, but not from that of the monotremes and at least one of the extinct multituberculate mammals (Kielan-Jaworowska 1975). In all marsupials in which they are present (they are not found in the Thylacine, *Thylacinus cynocephalus*), the epipubic bones project anteriorly from their articulation with the pubes at movable joints (Figs. 17.1 & 17.5). The paired bones lie in the ventral abdominal wall and the external and internal oblique muscles insert into them (Elftman 1928-9). The epipubic bones are believed to help support the abdominal wall and may have a function in protecting the pouch from excessive pressures.

Another feature regarded as a marsupial characteristic concerns the structure of the angle of the mandible. With the exception of the Honey Possum, *Tarsipes rostratus*, there is invariably a medially-directed shelf into which the internal
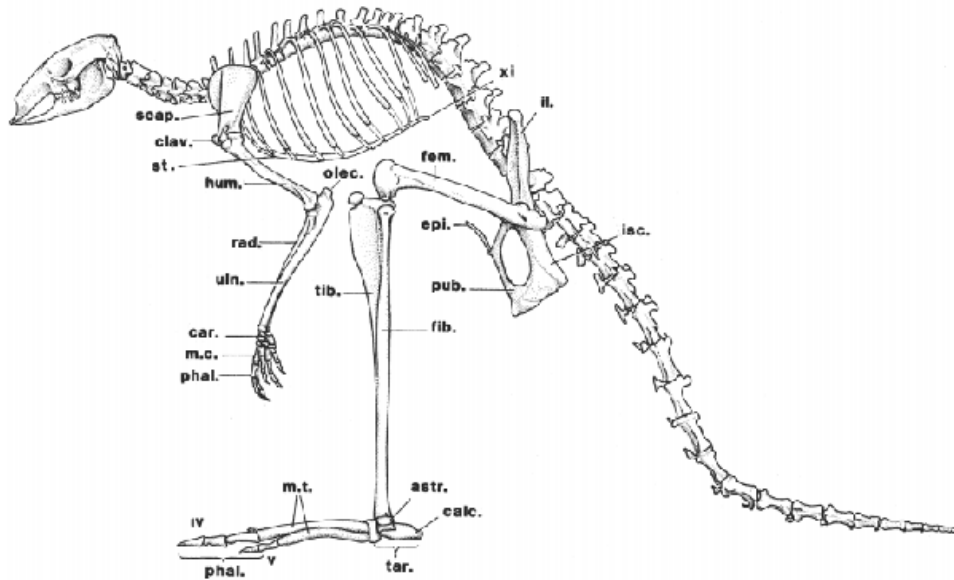
Figure 17.1 Lateral view of a macropodid skeleton; Key: astr. = astragalus; calc. = calcaneum; car. = carpals; clav. = calvicle; epi. = epipubic bone; fem. = femur; fib. = fibula; hum. = humerus; il. = ilium; isc. = ischium; m.c. = metacarpals; m.t. = metatarsals; olec. = olecranon process; phal. = phalanges; pub. = pubis; rad. = radius; scap. = scapula; st. = sternum; tar. = tarsals; tib. = tibia; uln. = ulna; xi. = xiphoid. (© ABRS)   [M. Thompson]

pterygoid muscle inserts (Fig. 17.3). This shelf, known as the inflected angle, varies in size from relatively small in carnivorous and insectivorous forms to extremely large in herbivores.

A further major diagnostic feature of the Metatheria is the almost total suppression of the deciduous dentition. Only a single deciduous tooth usually erupts and generally is regarded as the last premolar. On the basis of a detailed embryological study of the Yellow-footed Antechinus, *Antechinus flavipes*, however, Archer (1974, 1978a) contended that this tooth is the first molar (M1), which is shed early in life. This view is not yet accepted widely and hence is not followed in this account.

Three other morphological features also form part of the characteristic marsupial skeletal system (Fig. 17.3):

    1. the auditory bulla, the often inflated floor of the middle ear cavity is made up most frequently by the caudal extension of the alisphenoid, rather than the tympanic as in eutherians, and other bones, including the petrosal and squamosal, also may be involved;

    2. the jugal is prolonged back along the zygomatic arch to contribute to the anterior part of the glenoid fossa;

    3. the lacrymal bone not only forms part of the medial wall of the orbit, but also extends onto the face.

A further marsupial skeletal feature worth noting is found in the palate. The palatal portions of the premaxilla and maxilla are fenestrated by a series of usually paired openings or vacuities. Useful general references on marsupial osteology are Jones (1949), Grassé (1955) and Marshall (1962).
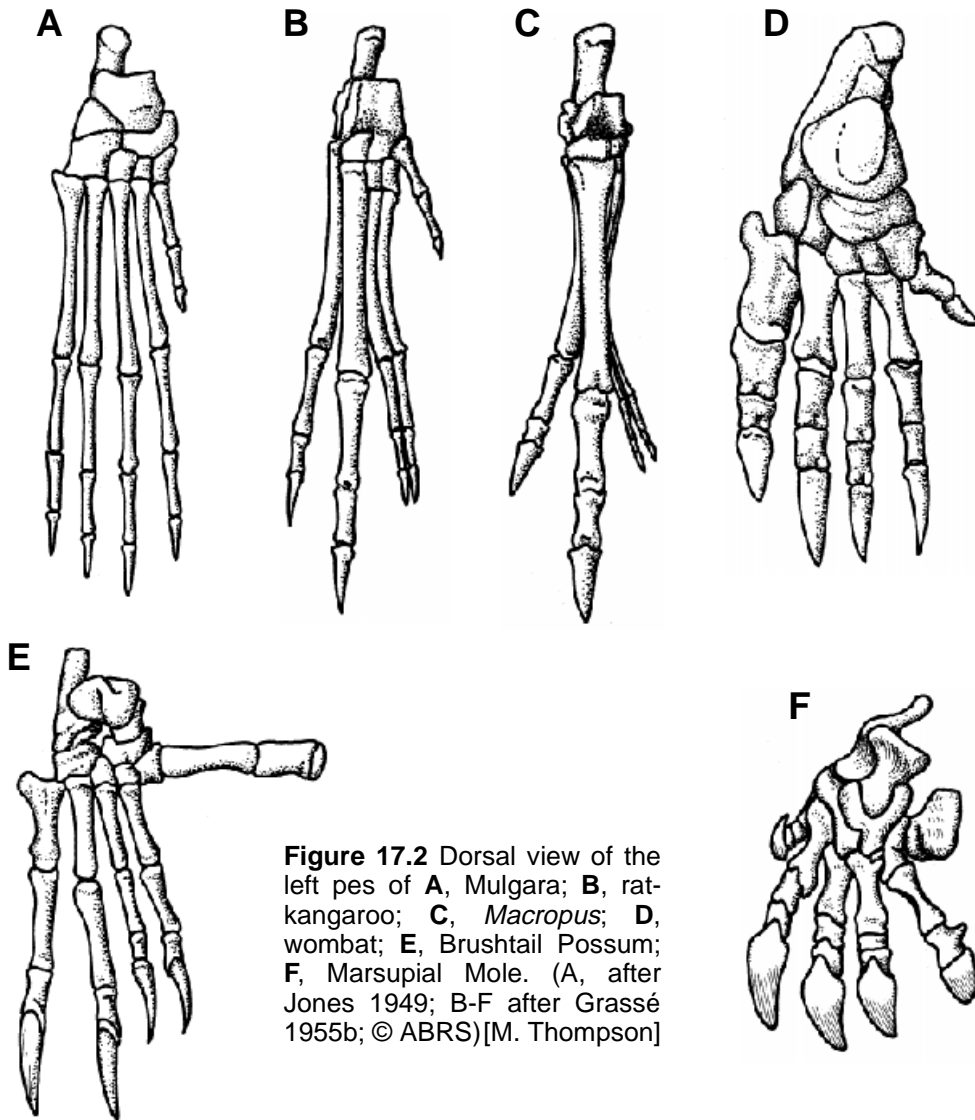
Figure 17.2 Dorsal view of the left pes of **A**, Mulgara; **B**, rat-kangaroo; **C**, *Macropus*; **D**, wombat; **E**, Brushtail Possum; **F**, Marsupial Mole. (A, after Jones 1949; B-F after Grassé 1955b; © ABRS)[M. Thompson]

Skull

Cranium. Relative to body size, the neurocranium of marsupials seems to be small compared with that of eutherians. The snout is variable in size, related primarily to feeding habits and is separated from the neurocranium by a narrowing of the cranium in the region of the orbits.

The occipital region is bounded dorsally by an occipital crest which may extend ventro- laterally on each side as a conspicuous ridge in carnivorous forms. In herbivores, the lateral crest is low, but is continued ventrally onto a well-developed paroccipital process from which a digastric muscle takes origin. An occipital condyle lies on each side of the posteriorly directed foramen magnum.

Much of the dorsal and lateral wall of the neurocranium is formed by the extensive parietal bone and a sagittal crest may be present to provide an additional attachment area for the temporal muscles. The squamosal completes the postero-ventral wall of the neurocranium and forms the greater part of the glenoid fossa for the articulation of the mandibular condyle. Carnivores typically show a well-developed postglenoid process. Posterior to the glenoid fossa lies the auditory bulla which shows a variable degree of inflation.

On the ventral part of the neurocranium side wall, the squamosal gives rise to the posterior half of the zygomatic arch. The anterior half is formed by the jugal bone, which extends back as a narrow tongue under the squamosal to form the

antero-lateral border of the glenoid fossa. The orbit and temporal fossa are confluent and are bounded ventro-laterally by the zygomatic arch. The medial orbital wall is largely composed of a downgrowth of the frontal bone, assisted by contributions from the large lacrimal and small, indistinct orbitosphenoid. A backward extension of the maxilla forms the orbital floor.

The neurocranium floor in the midline is composed of the basioccipital, basisphenoid and presphenoid, while more laterally there are contributions from the petrosal and alisphenoid bones. Most of the side wall of the snout is formed by the maxilla which carries the canine and cheek teeth. The lacrimal makes a small contribution postero-superiorly and the snout is completed anteriorly by the premaxilla which bears the incisor teeth. The roof of the snout is formed mainly by the two long nasal bones which characteristically broaden posteriorly. The nasal aperture is bounded by the nasals above and the premaxillae below and on each side. It leads into the large nasal chambers which house the scroll-like turbinal bones.

The palate is made up largely of the maxillae, with small contributions anteriorly and posteriorly by the premaxillae and palatines, respectively. It is penetrated anteriorly by the incisive foramina and posteriorly by a pair of large vacuities, but many other openings also may be found. Posterior to the hard palate are the two longitudinally disposed, wing-like pterygoid bones.

Mandible. The lower jaw comprises the two dentary bones which may or may not show fusion at the symphysis. Posterior to the tooth-bearing region of each dentary, the coronoid process extends up into the temporal fossa; it varies in size depending on the development of the temporal muscles. The mandibular condyle lies posterior to the coronoid process and articulates with the glenoid fossa. The condyles are almost at the level of the tooth row in carnivorous forms, but at a considerably higher level in herbivores. In carnivores, the condyle is cylindrical and transversely oriented, whereas in herbivores it is almost flat. The postero-lateral part of the dentary is concave for the insertion of the masseter muscle and, in macropodids, there may be a forward continuation of the cavity as a canal into which a slip of the masseter inserts. Postero-medially, the dentary also may be concave for the internal pterygoid muscle attachment. At its inferior edge there is the characteristic, shelf-like, medially-directed inflected angle.

Dentition. Unlike eutherian mammals, there may be only one functional deciduous tooth in marsupials. The permanent dentition includes the four mammalian tooth types: incisors (I), canines (C), premolars (PM) and molars (M).
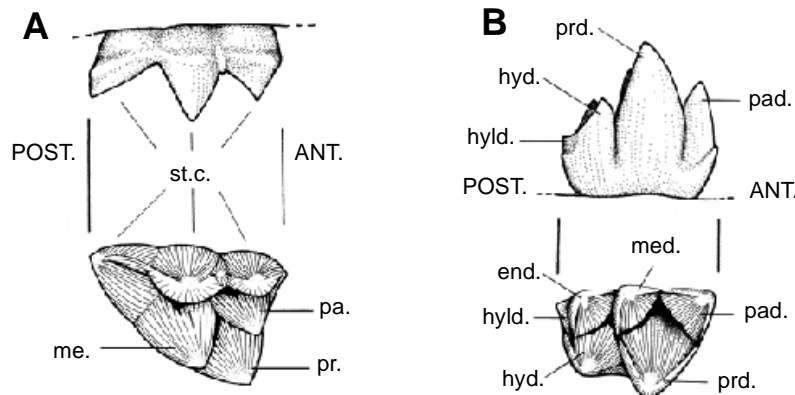

Figure 17.4 Lateral and occlusal view of an upper (A) and a lower (B) right molar tooth of the quoll; Key: end. = entoconid; hyd. = hypoconid; hyld. = hypoconulid; me. = metacone; med. = metaconid; pa. = paracone; pad. = paraconid; pr. = protocone; prd. = protoconid; st.c. = stylar cusps.(© ABRS) [M. Thompson]
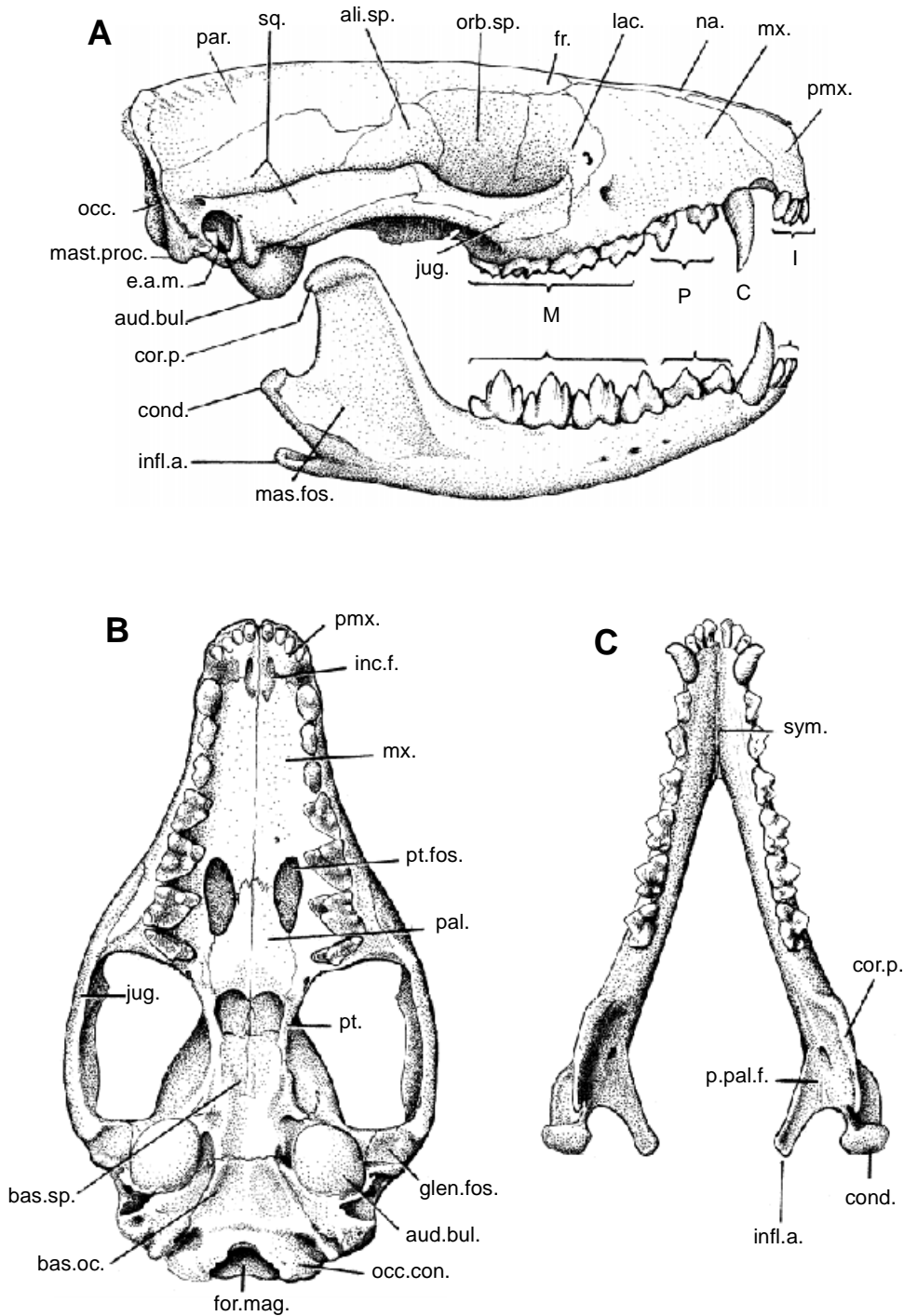
Figure 17.3 Skull of the quoll. **A**, Lateral view of cranium and mandible; **B**, ventral view of cranium; **C**, occlusal view of mandible; ali.sp. = alisphenoid; aud.bul. = auditory bulla; bas.oc. = basioccipital; bas.sp. = basisphenoid; C = canine tooth; cond. = condyle; cor.p. = coronoid process; e.a.m. = external auditory meatus; for.mag. = foramen magnum; fr. = frontal; glen.fos. = glenoid fossa; I = incisor teeth; inc.f. = incisive foramen; infl.a. = inflected angle; jug. = jugal; lac. = lacrimal; M = molar teeth; mas.fos. = masseteric fossa; mast.proc. = mastoid process; mx. = maxilla; na. = nasal; occ. = occipital; occ.con. = occipital condyle; orb.sp. = orbitosphenoid; P = premolar teeth; pal. = palatine; par. = parietal; pmx. = premaxilla; p.pal.f. = posterior palatine foramen; pt. = pterygoid; pt.fos. = pterygoid fossa; sq. = squamosal; sym. = mandibular symphysis. (© ABRS)   [M. Thompson]

The molar pattern is derived from the postulated three-cusped (tribosphenic) early mammal cheek tooth. In a modern marsupial upper molar, the three cusps (protocone, paracone and metacone) are arranged in the form of a triangle (trigon) and, in addition, a row of up to five small projections (stylar cusps) may be found along the outer border of the crown (Fig 17.4a). A lower molar shows a similar, but oppositely oriented, triangular arrangement (protoconid, paraconid and metaconid). A posterior extension of the tooth (the heel or talonid), however, forms a saucer-shaped area bounded by up to three small cusps (hypoconid, hypoconulid and entoconid) (Fig 17.4b). These molar tooth patterns are typical of insectivorous marsupials and, on occlusion, the large upper tooth protocone is pressed into the centre of the heel of the lower molar. At the same time, the other cusps slide against one another to form a series of small, sharp cutting surfaces. By these two mechanisms the insect food is simultaneously cut and crushed.

Amongst the larger carnivorous forms, there is a tendency for the molar cusps to be aligned antero- posteriorly on a narrowed tooth to produce a more efficient cutting blade. In contrast, the herbivores need a large, flat grinding surface. This is achieved by developing a fourth cusp and producing two transverse ridges which link the cusps in pairs. This arrangement results in an occlusal (biting) surface which may be used to cut, crush and grind vegetable material.

The basic number of teeth in marsupials would appear to be 50. In each half of the upper and lower jaws the dental formula is: I 5/4 C 1/1 PM 3/3 M 4/4. In extant Australian forms, however, the incisor numbers do not exceed 5/3. Dentitions in which numerous incisors are retained are termed polyprotodont and are characteristic of carnivores. Diprotodonty, which is found in herbivores, refers to reduction of the lower incisors to a single functional pair and with three or fewer pairs in the upper jaw. Herbivorous marsupials also tend to lose their canine teeth and the two anterior premolars. A long toothless gap (diastema) is formed between the incisors and the premolar in both jaws.

Certain macropodids which have become grazers are adapted to abrasive foods, such as grass, through erupting their molars sequentially. As the anterior cheek teeth wear down and are shed, fresh teeth appear at the back of the tooth row and the whole row moves forward (Sanson 1980). There is a different adaptation in the Vombatidae. Their teeth are open rooted which implies that, unlike all other marsupials, they grow continuously. As the biting surface wears, new tooth substance is formed at the base and the tooth is pushed up into occlusion.

Further modifications in tooth size or number are apparent in marsupials adapted to specialised foods such as nectar in the Honey Possum and termites in the Numbat.

Vertebral column

The vertebral column not only supports and gives stability to the body, but also serves for the attachment of trunk, limb and tail muscles (Fig. 17.1). The numbers of vertebrae in the five functional regions of the column are: cervical, as in virtually all mammals, seven; thoracic, 11–15; lumbar, four to eight; sacral, two to six; caudal, highly variable, from very short (as in the Koala) to extremely long (as in kangaroos and wallabies). The total number of trunk vertebrae is usually 19, but the relative numbers of thoracic and lumbar vertebrae are variable.

Cervical region. The first two cervical vertebrae (the atlas and axis, respectively) are concerned mainly with support and mobility of the head. The atlas typically lacks the centrum and is merely a ring of bone surrounding the spinal cord. Into its anterior border are excavated two large facets in which the occipital condyles of the skull articulate to allow vertical head movements. The axis, with the centrum of the atlas fused to its own, has a characteristically

elongated centrum (odontoid process) which lies within the ring of the atlas. The movement permitted between the atlas and axis is rotation. The interlocking articular facets on the anterior and posterior surfaces of the succeeding cervical vertebrae permit small generalised movements which, together, account for the overall flexibility of the neck and mobility of the head.

Thoracic region. These vertebrae are characterised by long dorsal spines to which body- bending muscles are attached. In addition, some of the head-supporting muscles extend from the back of the neurocranium, along the length of the neck to be inserted finally on the elongated dorsal spines of the anterior thoracic region. A pair of ribs articulates with each vertebra and is attached ventrally to the sternum by means of rib (costal) cartilages. The ribs are characteristically double-headed with one head resting against a process of the neural arch and the other against the vertebral body directly below, thus preventing excessive inward movements of the rib shafts when pressure is applied to the outside of the thorax.

Lumbar region. The lumbar vertebrae are solidly constructed and do not bear ribs (Fig. 17.5). They have stout dorsal and transverse processes and also may have midventral processes on the centra. The hip flexor muscles (psoas) take origin from the lumbar vertebral bodies.

Sacral region. The sacrum is formed by fusion of a variable number (two to six) of vertebrae with expanded transverse processes, which provides a solid support for the pelvic girdle (Fig. 17.5). Burrowing species have the largest number of sacral vertebrae.
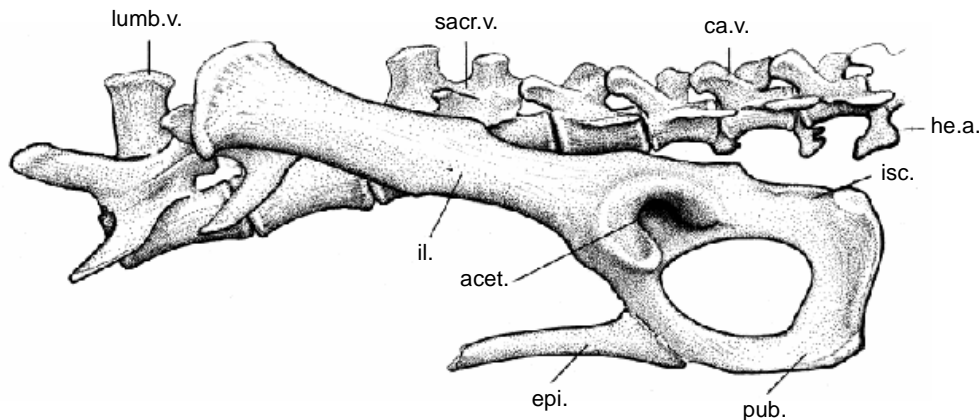

Figure 17.5 Lateral view (left) of the pelvis and adjacent vertebral column of *Trichosurus*; Key: acet. = acetabulum; ca.v. = caudal vertebra; epi. = epipubic bone; il. = ilium; lumb.v. = lumbar vertebra; pub. = pubis; sacr. = sacrum. (© ABRS)   [M. Thompson]

Caudal vertebrae. Marsupial tails vary from the long, powerful, balancing and supporting structure of the kangaroo (with up to 25 vertebrae) to the prehensile tail of the possum (with a similar number) and the koala, where the tail is virtually non-existent (Figs 17.1 & 17.5). The individual caudal vertebrae decrease progressively in complexity from the sacral end to the tip. Ventral haemal arches are commonly found just below the junctions between adjacent centra in the caudal region. The caudal vein and artery lie within these arches.

Forelimb and Girdle

Girdle. The forelimb girdle is composed of the clavicle and the scapula (Fig. 17.1). The clavicle links and positions the forelimb with regard to the vertebral column, by articulating with the sternum and the spine of the scapula.

It is well developed in most marsupials, but absent in the Thylacine and bandicoots of the genus *Perameles*. The scapula is a flat, triangular bone which features a long ridge-like spine (two in *Notorcytes*) on its outer surface. The spine is continued ventrally to articulate with the clavicle. At its ventrally directed apex, the scapula bears the glenoid fossa which receives the rounded head of the humerus.

Humerus. This is a stout bone, but its relative length and shape vary considerably with the locomotory and feeding habits of the species. The upper end, in addition to the rounded head, bears tuberosities for muscular attachments. The lower end is flattened, extended laterally and possesses a double articulation for the radius and ulna.

Radius and ulna. The radius, which is lateral to the ulna at the elbow, crosses over to be the inner of the two bones at the wrist. It is a slender bone and has a cup-shaped upper end for articulation with the humerus. The ulna has a large subterminal notch for humeral articulation. A stout protuberance, the olecranon process, permits extensor muscle attachment. The distal ends of the radius and ulna articulate with the carpal bones.

Carpus, metacarpus and phalanges. The carpals are a small group of irregularly shaped bones which form the wrist region. Most marsupials retain five clawed digits, each including a metacarpal and phalanges (three on each digit, except the first which has two). An extreme modification is found in the marsupial moles where, in the manus, the small digits I and II are folded across the palm against the greatly expanded and clawed third and fourth digits. The small fifth digit has only a small boss at its tip (Jones 1923a, 1924).

Hindlimb and Girdle

Girdle. As in all mammals, each half of the pelvic girdle consists of three fused bones (Fig. 17.5). The ilium lies almost parallel with the vertebral column and is attached firmly to the sacrum. The pubic and ischial bones extend downwards and backwards from their participation in the acetabulum, the socket for articulation of the femur. The pubic bones of the two halves of the pelvis meet and fuse at a fibrous joint in the midventral line. The characteristic epipubic bones articulate with the pubic bones and are directed anteriorly.

Femur. The marsupial femur is generally a strong, cylindrical bone in which the head is directed medially to fit into the acetabulum. The upper end of the bone includes bony projections (tuberosities), some of which may be large, for the attachments of the locomotory muscles. There are two large condyles on the expanded lower end of the bone which articulate with the head of the tibia.

Tibia and fibula. The flattened head of the tibia has two shallow depressions for articulation with the femoral condyles. The patella is an ossification in the tendons of the muscles which pass over the anterior surface of the knee joint (Fig. 17.8). The tibia is a substantial bone, whilst the fibula varies in size in different species but is always considerably smaller. Unlike eutherians, the marsupial fibula often has some contact (direct or via a cartilaginous disc) with the femur at the knee joint. It may also be involved in the ankle joint (Barnett & Napier 1953).

Tarsus, metatarsus and phalanges. Of the group of bones forming the tarsus, the astragalus articulates with the lower end of the tibia and usually the fibula, while the calcaneum extends backwards to provide an advantageous attachment lever for the calf muscles. The five digits are each composed of a relatively long metatarsal bone followed by three phalanges, except on the first digit which has only two. The first digit of Brushtail Possums is extremely robust and widely separated from the other digits to facilitate gripping branches in its arboreal habitat. The foot of saltators (for example *Hypsiprymnodon*) is considerably modified in that digit I is reduced, while II and III are very slender and closely

bound together by a skin envelope with only the claws free. Digit IV is enlarged considerably, but V is of medium size (Fig. 17.2). In the case of *Macropus*, the specialisation has proceeded even further. Digit I has been lost and digit IV is enlarged even more. These adaptations reduce the lateral mobility of the foot, but increase the functional length of the limb for ricochetal locomotion.

MUSCULAR SYSTEM

As in the osteology, marsupial myology tends to follow the basic mammalian pattern although there are a few unusual features. For example, the skin (dermal) musculature and the macropod masseter (a masticatory muscle) show characteristics not found in Eutheria. Few comprehensive descriptions of marsupial musculature are available, other than those of Barbour (1963) and Jones (1949). Useful accounts of limb muscles, however, have been given by Coues (1872), MacCormick (1887), Parsons (1896), Sonntag (1921a), Craven (1971) and Twomey (1975).

Skin

As in most mammals, the thin, subdermal panniculus carnosus is present and is extensive in marsupials, particularly over the anterior part of the head, neck and body. It has little or no attachment to bone. In the facial region there are, at least, slightly thickened portions around the eye and mouth and well-defined slips associated with the external ear movements. The part of the muscle layer on the side of the snout forms the buccinator and generally is attached to the adjacent maxilla and mandible and to the lips. It serves to hold the food between the teeth. On the ventral body wall there is a gap in the dermal musculature to allow the passage for the infolding of skin to form the pouch in the female and for the spermatic cord in the male. The muscle fibres surrounding the opening into the pouch may function to support, and even partly close, the pouch.

Masticatory muscles

(refer to Fig. 17.3 for bony attachments)

Temporalis. This large, fan-shaped muscle takes origin from most of the sidewall of the neurocranium and extends from just behind the orbit to the occipital crest. In some species, for example, the Tasmanian Devil, *Sarcophilus harrisii*, this origin may include a sagittal crest which gives increased bony surface for muscle attachment. The temporalis muscle fibres pass downwards, within the zygomatic arch, to insert into the inner and outer surfaces of the coronoid process of the mandible. The main function of this muscle is in fast, forceful jaw closure, especially in carnivores, where the canines must be driven into the prey.

Masseter. The fibres of this complex, powerful muscle, are arranged in a number of layers which may run in different directions and, hence, differ in the precise movements with which they are associated. The most superficial portion of the muscle is attached to the lateral surface of the snout below the eye and passes backwards to its insertion around the angle of the lower jaw. Contraction of these fibres results in jaw protrusion. The deeper fibres of the masseter attach to the lower lateral wall of the zygomatic arch and pass to the outer surface (masseteric fossa) of the mandible. In macropodids, and in extreme form in bettongs (*Bettongia*), the anterior part of the deep masseter is continued forward from the masseteric fossa and passes into a canal, where it finally attaches within the body of the mandible as far forward as the level of the first molar tooth. The main function of the deep masseter is slow, powerful, jaw closure and its unique forward prolongation is concerned with antero- posterior chewing movements.

Pterygoids. The external pterygoid is a relatively small deep muscle, originating from the pterygoid bone on the base of the neurocranium. It passes backwards and upwards to the mandibular condyle and neck and serves to stabilise the condyle in its socket, the glenoid fossa. The internal pterygoid muscle is considerably larger, especially in the macropodids. It runs backwards and downwards from the pterygoid bone to be inserted into the pterygoid fossa, which is bounded below by the inflected angle of the mandible. The two internal pterygoids work alternately and in cooperation with the deep fibres of the masseters, to produce sideways jaw movements. In macropodids, because the mandibular symphysis is unfused, simultaneous contraction of both internal pterygoids results in the divergence of the tips of the two lower incisors (Ride 1959). This allows the occlusion of the lower incisor against all three upper incisors on each side of the jaw.

Floor of the mouth, tongue and front of neck. The attachments of these muscles include the mandible, the hyoid bone (which lies just in front of the larynx) and the tongue. The tongue also has a complex set of internal (intrinsic) muscles and may be supported on its lower surface by a midline thickening of connective tissue, known as the sublingua. The most highly specialised tongue is that of the nectar-feeding Honey Possum. It is long, thin and contains tissue spaces (sinusoidal cavernous tissue) into which blood may be forced to act as a tongue stiffening mechanism. Amongst the muscles on the floor of the mouth is the digastric muscle with its intermediate tendon. This muscle passes from the base of the neurocranium near the auditory bulla, to the lower margin of the mandible and serves to lower the jaw.

Neck

On the ventral surface of the neck, muscles pass backwards from the hyoid bone to the sternum (sternohyoid) and the scapula. On each side of the neck others run from the mastoid process to the sternum (sternomastoid) and to the clavicle (Fig. 17.6). Also a ventro-lateral group of muscles passes between the neck vertebrae and the ribs. At the back of the neck some small deep muscles link the base of the neurocranium to the atlas and to some of the other cervical vertebrae. These muscles are concerned mainly with head and neck movements.

Thorax and Abdomen

Filling each of the rib spaces of the thorax are three layers of intercostal muscles. They are of importance for respiratory movements. There is a similar set of three sheet-like abdominal muscles. The most superficial is the external oblique which passes from the middle of the back to insert ventrally in the midline (linea alba) of the abdomen (Fig. 17.6). The fibres of each layer, like those of the intercostal muscles, run in different directions to give strength. They function to support the abdominal viscera. The midventral part of the abdomen is supported additionally by the strap-like rectus abdominis, which extends from the first rib cartilage back to the epipubic and pubic bones, and also by the pyramidalis, characteristically very large in marsupials. The pyramidalis muscle has a long attachment stretching from the epipubic bones and the surface of the rectus abdominis. It inserts in the midline from the pubic symphysis to the cartilaginous process (the xiphoid) at the posterior end of the sternum.

Deep Neck and Back; the Tail

A large and complex set of long and short muscles stretch between individual and groups of vertebrae to facilitate bending of the cervical, thoracic and lumbar vertebral column. These muscles also have attachments to the ribs, pelvis and base of the neurocranium. The movements of the tail are controlled by another

series of muscles. At the root of the tail they attach to the pelvis and sacrum and insert at variable distances along the tail. Within the tail various muscles may either run between successive vertebrae, for short lengths or even along the full length of the tail.

Forelimb and Girdle

The main movements with which the limb muscles are concerned include flexion (bending), extension (straightening), protraction (moving limb forward), retraction (pulling limb backwards), rotation, abduction (moving away from the midline) and adduction (moving towards the midline).

Usually about 11 muscles run from the trunk (axial) skeleton to the humerus, scapula and clavicle (Fig. 17.6). The pectoralis major (and also the pectoralis minor which lies deep to it) passes from the sternum, ribs and sometimes also the clavicle, to the humerus. At its insertion, the pectoralis major may be joined by the panniculus. The pectoralis muscles are concerned mainly with protracting the limb. The third pectoralis muscle (pectoralis quartus) originates from the linea alba and the panniculus, an attachment which is apparently typical of marsupials (Barbour 1963). It also inserts on the humerus. The extensive latissimus dorsi muscle passes laterally and forwards from the thoracic spines to its insertion on the humerus. It functions to retract the forelimb. The trapezius, another large dorsal muscle, has an extensive origin stretching from the posterior wall of the neurocranium and from the spines of the cervical and most of the thoracic vertebrae. Its insertion is similarly great and may include the clavicle, scapular spine and even the humerus. This muscle stabilises the scapula
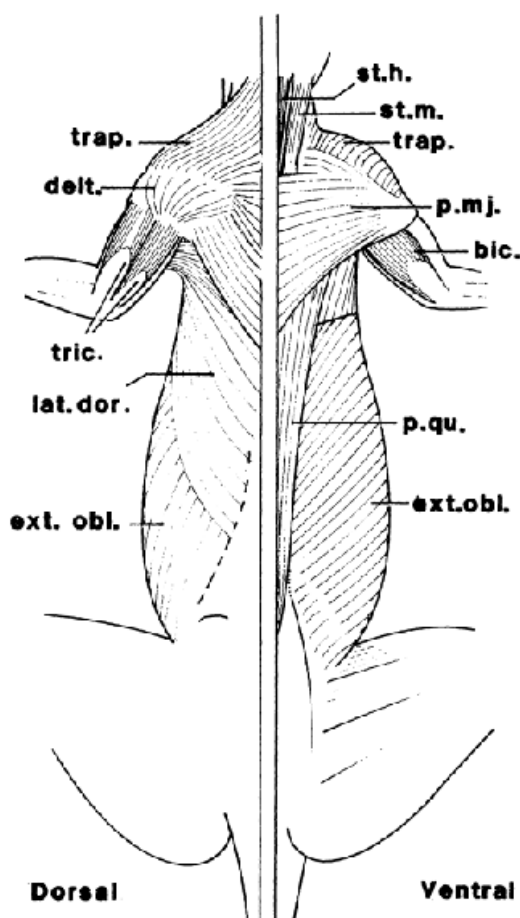

Figure 17.6 Dorsal and ventral superficial trunk muscles of the Quokka. (Modified from Barbour 1963); Key: bic. = biceps; delt. = deltoid; ext.obl. = external oblique; lat.dor. = latissimus dorsi; p.maj. = pectoralis major; p.qu. = pectoralis quartus; st.h. = stylohyoid; st.m. = stylomastoid; trap. = trapezius; tric. = triceps.(© ABRS)   [M. Thompson]

and, in addition, its anterior fibres assist in protracting the limb, while the posterior fibres participate in its retraction. The serratus anterior (magnus) and the levator scapulae may be continuous and originate from the transverse processes of the last few cervical vertebrae and up to about eight of the ribs. Their insertion is on the inner surface of the dorsal (vertebral) border of the scapula. These muscles and the pectorales serve to suspend the anterior part of the body in a muscular sling which acts as a shock absorber when the forelimbs hit the ground during locomotion (Fig. 17.7).
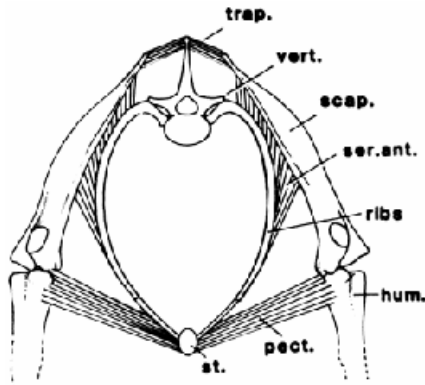

Figure 17.7 Body supporting muscles of the forelimb. ; Key: hum. = humerus; pect. = pectoral muscles; scap. = scapula; ser.ant. = serratus anterior; st. = sternum; trap. = trapezius; vert. = vertebra.(Modified from Slijper 1946; © ABRS)   [M. Thompson]

Five muscles pass from the scapula to the upper end of the humerus. They stabilise the shoulder joint and also have functions in the basic movements of the limb. In addition, the bulky deltoid muscle attaches to the clavicle and the scapular spine, passing over the shoulder joint to attach to the humerus (Fig. 17.6). It is a large muscle divided into anterior, middle and posterior parts which are concerned with protraction, abduction and retraction, respectively.

The prominent muscle on the front of the upper arm is the biceps brachii which may be subdivided to form two separate muscles (Fig. 17.6). It attaches to the scapula superiorly and inferiorly to both the radius and ulna. The biceps and a smaller muscle below it, the brachialis, are the flexors of the elbow joint. The antagonist to these muscles is the powerful triceps brachii, lying at the back of the upper arm (Fig. 17.6) and running from the scapula and humerus to the olecranon process, the backward- projecting portion of the ulna.

The two main groups of muscles in the forearm are concerned with flexing and extending the wrist, palm and finger joints. The muscles of flexion take origin mainly from the medial (inner) side of the lower end of the humerus and the medial parts of the radius and ulna. The muscles of extension originate principally on the outer part of the lower end of the humerus and the adjacent outer parts of the radius and ulna. Both groups of muscles insert into various parts of the carpal, metacarpal and digital bones. Other muscles in the forearm pass between the radius and ulna and function to rotate the forearm and manus. Numerous small muscles within the manus act to flex, draw together, or separate the digits.

Hind Limb and Girdle

There is considerable variability between species in many of these muscles with regard to relative size, origin and insertion. Names of these muscles also differ between authors. Interconnections between muscles, additional muscles or separation of parts of muscles commonly are reported.

The psoas minor passes from the ventral surfaces of the thoracic and lumbar vertebrae to the inside of the pelvis. The relatively smaller psoas major runs from the lumbar and sacral vertebrae to the upper end of the femur. The former muscle bends the vertebral column and the latter flexes the femur at the hip joint.

The hip region musculature include the iliacus, which comes from the inside of the pelvis and joins the psoas major at its insertion to flex the hip joint. An important group of muscles, the gluteal muscles, arise mainly from the external surface of the pelvis (the ilium) and are associated principally with abduction and extension at the hip joint. The gluteus maximus, the most superficial of these muscles, is a thin sheet which inserts on the lateral side of the upper part (greater trochanter) of the femur, but also has a flat tendinous portion (tensor fasciae lata) which passes down the lateral side of the thigh to attach to the tibia and fibula. The gluteus medius lies deep to the maximus and is a large thick muscle which attaches above to most of the external surface of the ilium and is inserted on the femur into the upper end (greater tuberosity). The gluteus minimus and quartus, when present, are small muscles with similar attachments and functions to the other glutei. In addition, there is a small group of muscles which is mainly concerned with stabilising the hip joint and rotating the femur (and hence the whole lower limb). A thick strong muscle, the quadratus femoris, passes backwards from the ischium to the femur and assists in extension movements.

The front of the thigh includes both hip flexors and knee extensors. The sartorius and rectus femoris cross both the hip and the knee joints and are capable of performing both, flexion and extension. The main bulk of the anterior thigh muscles is made up of the quadriceps femoris muscle group. Of this group, the rectus femoris has its origin on the ilium, whereas the other three muscles (the anterior, medial and lateral vasti) originate on the shaft of the femur. Thus the vasti, which show various degrees of fusion, only flex the knee joint. All four muscles insert via a common tendon, which encloses the patella, into the upper end of the tibia (Fig. 17.8). The sartorius lies superficial to the quadriceps and may be well developed. It passes from the ilium to insert on the upper medial part of the tibia, but with a slip into the quadriceps tendon.

An important group of three muscles lies at the back of the thigh and takes its main origin from the ischial tuberosity or the adjacent ischium. These muscles are the main extensors of the hip joint and flexors of the knee joint. Of these muscles, the large biceps femoris muscle has an additional origin from some caudal vertebrae and its basic insertion is on the outer side of the upper end of the tibia, although it also extends onto the leg. The semitendinosus is a bulky muscle which inserts on the inner side of the upper end of the tibia. The third muscle, the semimembranosus, has an extensive origin from the ischium and inserts on the medial side of the upper tibia. On the inner part of the thigh there
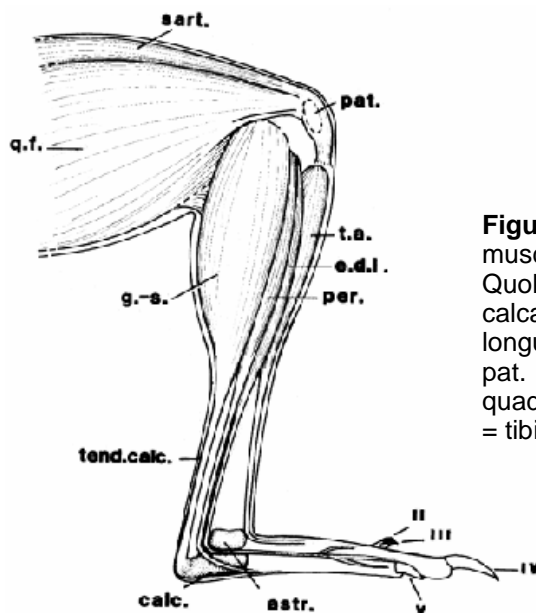

Figure 17.8 Lateral view of the muscles of the hind limb of the Quokka. astr. = astragalus; calc. = calcaneum; e.d.l. = extensor digitorm longus; g.-s. = gastrocnemius-soleus; pat. = patella; per. = peroneus; q.f. = quadratus femoris; sart. = sartorius; t.a. = tibialis anterior. (© ABRS)

[M. Thompson]

is a group of muscles primarily involved in adduction. The three main muscles, the adductors longus, brevis and magnus, vary in relative size and may be separate or fused into a single mass. Their origin(s) include the pubis and ischium from the symphysis to the ischial tuberosity and sometimes also the epipubic bone. The muscles have an extensive insertion on much of the back of the femur but also down to the upper end of the tibia. Because of this attachment, the adductors may also have an important extension action. A fourth adductor, gracilis, also passes from the pubis to the back of the femur. The pectineus, from the pubis and the epipubic bone, runs to the same region and has a similar adducting function.

The anterior leg muscles are mainly ankle and digit extensors, which dorsiflex (bend upward) the foot at the ankle joint and straighten (extend) the toes (Fig. 17.8). The posterior group of muscles are flexors and plantarflex (bend downwards) the foot at the ankle joint and bend (flex) the toes. Other anterior leg muscles act to stabilise or to angle (evert and invert) the foot at the ankle.

On the front of the leg the prominent tibialis anterior attaches to the upper part of the antero-lateral surface of the tibia and passes down to insert on the tarsal bones and in some cases also on the first metatarsal. The two long digital extensors run from the upper parts of the tibia or fibula (extensor hallucis longus) and tibia and fibula (extensor digitorum longus) to insert on the digits. On the lateral side, the peroneus muscles (separate or fused) take origin from the upper lateral part of the fibula. When separate, the tendon of the peroneus longus passes around the lateral side of the ankle and across the foot to insert on the first metatarsal. The peroneus brevis inserts on the fifth metatarsal. There is considerable variability in this muscle group.

At the back of the leg the large gastrocnemius-soleus complex (the soleus may or may not be distinct) takes its main origin from the medial and lateral condyles at the lower end of the femur. The two parts unite and near the ankle form the powerful tendon (tendo calcaneus) which inserts mainly on the calcaneum. It is a strong plantar flexor of the ankle joint. The plantaris muscle, when present, is associated with the lateral part of the gastrocnemius at its origin, but it passes over the calcaneum, inserting on the sole of the foot. The long digital flexors vary considerably in name and arrangement. In the Mulgara, *Dasycercus cristicauda*, for example, two muscles take origin from the fibula and tibia and pass to the lateral four and the medial one digit, respectively (Jones 1949). The tibialis posterior muscle is a very small muscle which originates on the upper part of the fibula. A long tendon passes to its insertion on the plantar surface of the foot. The last major posterior leg muscle is the popliteus muscle which lies deep, is generally well developed and passes from the fibula (and often also the femur) to the tibia.

The sole of the foot include a series of small muscles which are concerned mainly with flexing the digits and interphalangeal joints. They also adduct and abduct the toes.

LOCOMOTION

General Principles

Modes of movement among marsupials include fast running (dasyurids and bandicoots), hopping (kangaroos), climbing (the Koala, possums), gliding (gliding possums) and burrowing (marsupial moles).

While there are many adaptations for movement in animals, the mechanical principles underlying locomotion also limit what can be achieved. The work of Taylor, Schmidt- Nielsen & Raab (1970) provided the first comprehensive insight into the energetic costs of terrestrial locomotion. All types of locomotion

are better understood now and the considerable recent progress has been summarised in Fedak, Heglund & Taylor (1982); Heglund, Cavagna & Taylor (1982a); Heglund *et al*. (1982b); and Taylor, Heglund & Maloyi (1982).

For most mammals, the energy consumed during running and walking is related largely to speed and body mass. Taylor *et al*. (1982) have derived a general equation to describe these metabolic costs:

Energy expenditure (in watts) $= 10.7M_b^{0.684}\, V + 6.03M_b^{0.697}$

M_b is body mass in kilograms and V is speed in metres per second. The total cost of locomotion increases for larger animals, but the cost to move one kilogram of body mass decreases with increasing mass. The relative cost of carrying extra reserves of fat or water thus decreases with increasing body size and these reserves will last longer.

With this established base-line for the generalised costs of running and walking, it is possible to examine the mechanisms by which other modes of locomotion depart from it. Cursorial or fleet- footed animals, such as gazelles, are found to run relatively economically, while slower animals, such as man, have higher costs of locomotion. Except for the saltators, the marsupials do not seem to differ from other mammals in their costs of locomotion, although earlier work had suggested that this might be so (Baudinette, Nagle & Scott 1976a).

Locomotion in kangaroos

What are the characteristics of hopping and why is it so rare in large animals? At speeds below 6 km/ h, kangaroos do not hop, but adopt an odd gait. Weight of the body is supported alternately by the hind legs or the small front legs in concert with the tail. This walking gait is clumsy and energetically costly (Dawson 1983). Kangaroos resort to this mode of locomotion at low speeds because it would be even more costly to hop. Small hopping animals use simple quadrupedal locomotion at low speeds, but kangaroos are precluded from this option by the specialisation of their hind limbs and the reduction in size of their forelimbs.

At high speeds, hopping has advantages over running. Once hopping starts, the energetic costs do not change over a wide range of speeds. In treadmill experiments, when kangaroos hopped at speeds above 15 km/h, they travelled more economically than running animals (Fig. 17.9). This pattern of energy expenditure appears to be explained by the combination of a fixed hopping rate and the storage of energy in elastic elements such as tendons. Energy can be stored in such elastic fibrous tissues in much the same way as it is stored in a spring.

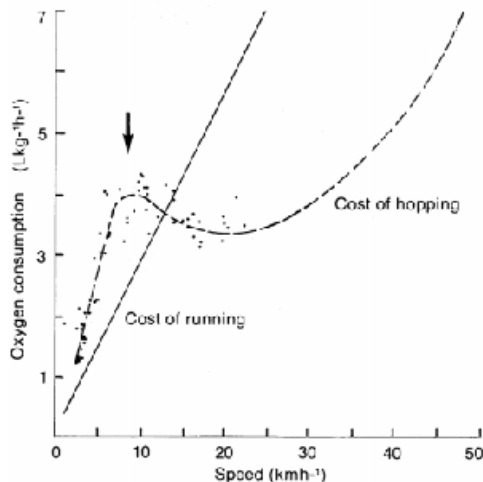**Figure 17.9** Changes in oxygen consumption with speed as a measure of the energetic cost of hopping in kangaroos. This is compared with the cost of running in quadrupeds and bipeds. The transition from walking to hopping is shown by the arrow. The solid line indicates the generalised cost of running for a eutherian mammal about the size (18 kg) of the kangaroos used in the study. (After Dawson 1983)

Animals in the wild probably travel at their most comfortable or economical speed. For kangaroos this appears to be about 20–25 km/h. Energy costs probably increase above this speed because there must be limits to the elastic storage of energy. Hopping rate, however, remains constant up to about 40 km/h with the increase in speed achieved by increasing the length of the stride. Kangaroos can increase their speed above 40 km/h and speeds up to 65–70 km/h have been reported. At these speeds there is a noticeable increase in stride frequency as well as stride length and this is probably accompanied by a marked increase in energy consumption.

Hopping may have evolved to take advantage of the apparent high metabolic scope of marsupials (Dawson & Dawson 1982); kangaroos increase their aerobic metabolism by more than 20 times during hopping. As a mode of locomotion, saltation must have adaptive advantages, in spite of its shortcomings at low speed. Kangaroos and other hopping macropodoids have radiated widely throughout Australia and many species have survived the impact of Aboriginal and European man.

Other forms of locomotion in marsupials

Many marsupial species are mainly arboreal and exhibit morphological adaptations appropriate to this life-style. These adaptations vary from the very specialised grasping forepaws of the Koala, to the gliding membranes (or patagia) of the gliding possums. The primary energetic cost of life in the trees is the mechanical work of lifting the body. Whether for a pygmy-possum or a tree kangaroo, this work is a product of body size, gravitational acceleration and the height climbed ($M_b \times g \times h$; Calder 1984). If the efficiency is the same, the energy expended in raising one kilogram one metre will be the same for all climbers. While the costs of transporting a unit mass on the level is greater for smaller animals, this is not the case for climbing and, in fact, the proportional increase in energy demand in climbing, over that required at rest, is lower for a smaller animal. A 24 g pygmy-possum would need to increase its metabolism to 2.7 times its resting basal level to climb 1 metre in 5 seconds. A tree kangaroo (7.4 kg), on the other hand, would need to increase its metabolism to 7.8 times its basal level to carry out the same work. Small animals, therefore, are less constrained by the costs of climbing. Larger species, such as the Koala, generally must climb slowly or, like some of the tree kangaroos, use trees only for limited periods.

Gliding appears to be an adaptation to overcome some of the energetic problems of climbing. It also allows for faster foraging and predator avoidance in more open forests.

The Marsupial Mole, *Notoryctes typhlops*, burrows or 'swims' through the desert sand with the aid of two flattened claws on its front feet. Almost nothing is known about the physiology or the energetic costs of movement in this marsupial, but burrowing is known to be a very costly form of locomotion in the eutherian burrowers (Vleck 1979).

FEEDING AND DIGESTION

While all three principal feeding types, *viz.* carnivory, omnivory and herbivory, are displayed abundantly among marsupials (Hume 1982), definition of the limits of each type is difficult. For instance, many carnivores are known to eat some plant material, either regularly or seasonally, when prey species may be scarce or unavailable. Conversely, herbivores may ingest some insect material that happens to be on the surface of food plants. In relatively few cases can a

marsupial species be described as a strict carnivore or strict herbivore. Natural dietary habits, however, do provide a convenient means of categorisation for the purposes of general discussion.

Carnivores

Four Australian marsupial families can be described as carnivorous. These are the Dasyuridae, Notoryctidae, Myrmecobiidae and Thylacinidae, of which the latter two are monotypic. The Numbat, *Myrmecobius fasciatus,* is insectivorous. Its diet consists mainly of termites; ants make up to 15% of the diet, but the bulk of these are small predatory species which are probably ingested incidentally as they swarm in to prey upon termites exposed when their nest is broken open by foraging numbats. *Notoryctes typhlops* feeds on subterranean insects and insect larvae, but some yam-like roots also may be eaten and opportunistic carnivory probably prevails. the Thylacine, which is considered extinct, fed on mammals such as rats, echidnas, wallabies and other small marsupials, birds and possibly lizards.

Among the Dasyuridae, the smaller members such as *Antechinus* species and *Planigale* species are almost wholly insectivorous, although some frogs and small reptiles may also be taken. Of the larger dasyurids, the diet of the Tasmanian Devil, *Sarcophilus harrisii*, is the best studied because of its reputation among farmers for killing domestic stock. Buchmann & Guiler (1977), however, concluded that Tasmanian devils were inept killers and appeared to be versatile scavengers rather than hunters. Their diet includes native fauna, such as wallabies, pademelons and birds, and introduced rabbits and sheep, the latter mainly as carrion. The diets of the native cats *Dasyurus viverrinus* and *D. geoffroii*, are more varied and include insects and lizards as well as small mammals and birds. Plant material, mainly grasses, herbs and blackberries, is also a common component of their diets. The larger Tiger Quoll, *Dasyurus maculatus*, is well known for its climbing ability. This is reflected in the higher incidence of birds and bird eggs in its diet. *Phascogale* species also are very active arboreally, but less is known about their natural diets.

Omnivores

The two groups of omnivorous Australian marsupials, the terrestrial bandicoots and bilbies and the arboreal possums and gliders, feed on a mixture of arthropods, fruits and plant exudates such as sap and gum. The Musky Rat-kangaroo, *Hypsiprymnodon moschatus*, is probably more accurately classified as an omnivore, but is discussed below along with the predominantly herbivorous rat-kangaroos.

The major food items of the bandicoots (family Peramelidae) are invertebrates such as insects, earthworms and insect larvae and plant materials such as fruits and roots. The bilbies (family Thylacomyidae) appear to be similar in their food habits. No apparent preference exists for any particular dietary item, the diet reflecting seasonal and temporal changes in availability of the various plant and animal components.

The arboreal omnivores include possums, such as Leadbeater's Possum, *Gymnobelideus leadbeateri*, and the smaller pygmy-possums *Cercartetus* species. The Mountain Pygmy-possum, *Burramys parvus*, also should be included in this group, which also includes species such as the Feathertail Glider, *Acrobates pygmaeus*, the Sugar Glider, *Petaurus breviceps*, the Squirrel Glider, *P. norfolcensis* and the Yellow-bellied Glider, *P. australis*. The group's principal protein supply comes from arthropods such as tree crickets, scarab beetles and moths. Non-foliage plant materials such as fruits, nectar, seeds and plant exudates high in soluble carbohydrates constitute the remainder of their
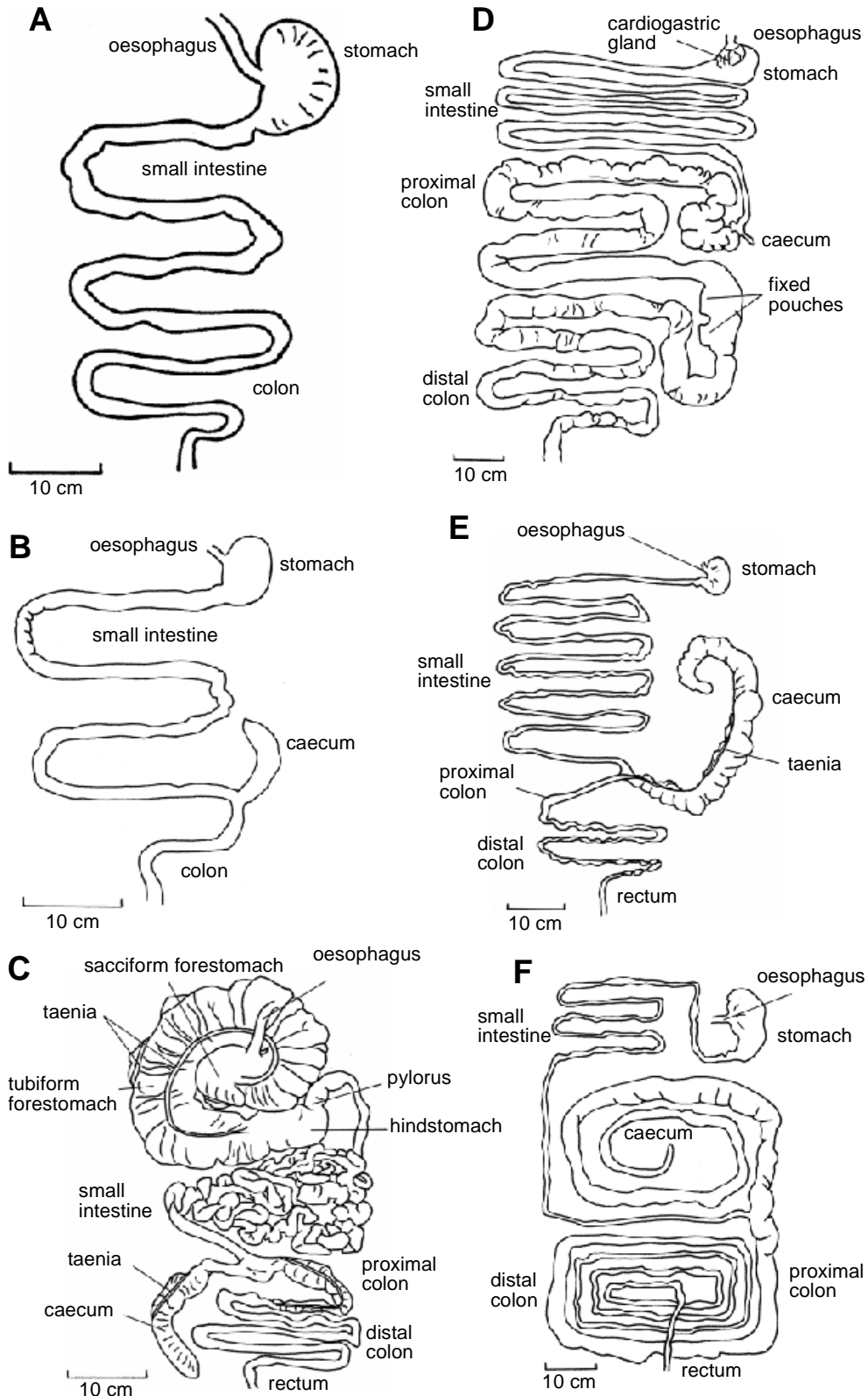
Figure 17.10 Comparative morphology of the digestive tract of various marsupials; a, the carnivorous Tiger Quoll (*Dasyurus maculatus*), showing short, undifferentiated intestine and absence of a caecum; b, the omnivorous Long-nose Bandicoot, showing differentiation of the hindgut into caecum and colon; c, the herbivorous Eastern Grey Kangaroo (*Macropus giganteus*), showing the large differentiated stomach and long small intestine, caecum and colon; d, the herbivorous Common Wombat (*Vombatus usinus*), showing the very enlarged large intestine of a hindgut fermenter; e, the folivorous Greater Glider (*Petauroides volans*), also a hindgut fermenter but in this case the caecum is enlarged; f, the folivorous Koala (*Phascolarctos cinereus*), with an enlarged caecum and proximal colon. (© ABRS)   [K. Hollis]

diet. Exudates include eucalypt sap, *Acacia* gum, manna (deposits of encrusting sugars at the feeding sites of sap-sucking insects) and honeydew, the excess sugars secreted by sap-sucking insects.

Herbivores

Herbivorous marsupials consist of two groups. The first group contains the terrestrial kangaroos, wallabies and rat-kangaroos (Superfamily Macropodoidea) and wombats (Family Vombatidae). The second group contains the arboreal folivores and includes the Koala, the Greater Glider, *Petauroides volans*, brushtail possums *Trichosurus* species, ringtail possums *Pseudocheirus* species, the Grey Cuscus, *Phalanger intercastellanus,* and tree-kangaroos *Dendrolagus* species.

The wombats are primarily grazers, feeding on both grasses and grass roots. Their teeth, adapted to an abrasive diet, are rootless and grow continuously throughout life. Macropodoids can be divided into grazers, browsers and an intermediate group. This division is based on dental morphology and an incomplete knowledge of natural dietary preferences. The molar teeth of grazers are characterised by strong links (longitudinal ridges) between the transverse lophs so that the surface area of upper and lower molars in contact at maximal occlusion while chewing is reduced, resulting in primarily a cutting action. This is an ideal adaptation for chewing abrasive, siliceous grasses, often of high fibre content.

In contrast, in the molar teeth of browsers the links are weaker, resulting in an increased surface area of contact of upper and lower molars during chewing. This produces more of a crushing action, ideal for softer, relatively unabrasive, lower-fibre leaves of shrubs and trees.

Grazers include the large red and grey kangaroos (*Macropus* species), smaller wallabies within that genus and nailtail wallabies *Onychogalea* species, hare-wallabies *Lagorchestes* species, and the Narbalek, *Petrogale concinna*, a rock wallaby. Browsers include the Swamp Wallaby, *Wallabia bicolor*, the Quokka, *Setonix brachyurus*, and the genera *Dendrolagus*, *Thylogale* and *Lagostrophus*. The rock wallabies, *Petrogale* species, fall into an intermediate category in both dental morphology and dietary habits.

The other macropodoid family, the Potoroidae (the rat-kangaroos), differs from the kangaroos and most wallabies in having a smaller body size and by feeding on plant materials of low fibre content. These include underground storage organs such as swollen tap roots, tubers and rhizomes as well as hypogeous (underground) fungi, grass seeds and some insect material. Insect material probably constitutes the main part of the diet of the smallest of the rat-kangaroos, the Musky Rat-kangaroo, which is found only in the tropical rainforests of northern Queensland.

Among the arboreal folivores, the Koala and the Greater Glider, *Petauroides volans*, are the most specialised feeders, accepting the foliage of only a limited number of *Eucalyptus* species. *Petauroides volans* also includes eucalypt flowers in its diet. The ringtail possums, *Pseudocheirus* species are also folivorous, but feed on the foliage of both eucalypt and non-eucalypt species as well as fruit of understorey species, when available. The brushtail possums, *Trichosurus* species are more generalist feeders, spending a significant proportion of their foraging time on the ground, feeding on the herb layer. The cuscuses and tree-kangaroos are inhabitants of tropical rainforests and feed on a mixture of tree foliage and fruits (Smith & Hume 1984).

DIGESTIVE SYSTEMS

Carnivores

The degree of complexity of the digestive system of mammals is inversely proportional to the ease with which the components of their natural diets can be digested. Carnivores are thus universally distinguished from nearly all omnivores and herbivores by their simple gut morphology. The stomach has no specialised blindsacs or diverticula in which ingested food could be retained long enough for microbial fermentation, although it is quite often distensible in those species which feed on large prey items. The small intestine is short, as is the large intestine. The colon is usually of similar diameter to that of the small intestine and the caecum is usually small.

Carnivorous marsupials differ from this general description in the complete absence of a caecum (Fig. 17.10a). This appears to be an example of secondary loss of a primitive organ which was derived from reptilian ancestors (Hume 1982).

The generally highly digestible nature of carnivore diets is reflected not only in a short, uncomplicated digestive system, but also in rapid transit of food through the gut. For example, a Dusky Antechinus (*Antechinus swainsonii*), fed on a mixture of ground house mice and termites, eliminated 90% of the indigestible termite heads in the faeces within 12 hours and 99% within 18 hours (Cowan, O'Riordan, & Cowan 1974).

Omnivores

The ingestion of plant material usually means that greater amounts of indigestible residues pass through the gut. The important nutritional consequences of this include a need for greater lubrication to protect the gut lining from physical damage and additional substrates for resident bacteria in the large intestine, particularly the caecum. The omnivore differs from the carnivore in that salivary glands are often larger (saliva having a lubricating function), the caecum has an increased capacity and there is an increase in the length of the small intestine, the colon or both (Fig. 17.10b).

Consistent with the greater length and capacity of the omnivore gut, digesta passage times are increased. Northern Brown Bandicoots, *Isoodon macrourus*, fed on termites require 29 hours for complete elimination of indigestible exoskeletons in the faeces (Waring, Moir & Tyndale-Biscoe 1966).

The Sugar Glider, *Petaurus breviceps*, and Leadbeater's Possum, *Gymnobelideus leadbeateri*, have been found to have a larger caecum and a longer colon than most other omnivores, marsupial or eutherian. These are both species that feed extensively on gums secreted by *Acacia* species which, if similar to gums of other tree species, may require microbial fermentation to be digested. This would explain the increased development of the caecum and colon in both these marsupials. A similar explanation has been suggested for the long caecum in several species of lemurs which also feed extensively on secreted gums.

Herbivores

The digestive system of herbivores is usually much more complex than that of omnivores, with the enlargement of certain regions of the gut to increase the retention time of digesta. This, in turn, allows time for the slow process of microbial fermentation of plant cell wall material (cellulose), often the bulk of the herbivore's diet, to take place. Fibre is a source of energy which is not available to vertebrates unless they have a complex digestive system to house

the dense microbial population which ferments cellulose and other components of plant cell walls. Herbivorous marsupials may be conveniently divided into two groups on the basis of the principal site of microbial fermentation. The foregut fermenters, in which the forestomach is greatly expanded, include the families Macropodidae and Potoroidae. The hind gut fermenters include the Vombatidae and the arboreal families Phascolarctidae, Phalangeridae and Pseudocheiridae.

The macropodid stomach is a long, basically tubular organ, extensively haustrated along the greater curvature (Fig. 17.10c). It can be divided into the forestomach (the region of microbial fermentation) and the hind stomach (the acid-secreting region of the gastric pouch and the adjacent mucus-secreting region terminating at the pylorus). The forestomach can be further divided into the sacciform forestomach (the region adjacent to, and the cul-de-sac oral to the cardia) and the tubiform forestomach (the main tubular body of the organ).

The small intestine is much longer than that of omnivores. The caecum and proximal colon are expanded to form a secondary area of microbial fermentation in the hind gut. The contribution from this fermentation area to the nutritional economy of the animal is minor compared with that of the forestomach (Hume 1982). The time for complete elimination of a meal in a herbivore is usually very long. This is because each meal is retained in some part of the gut so that a fraction of it is mixed with one or more following meals. Because of this feature of herbivores the term 'mean retention time' (MRT) has been adopted as the best comparative measure of the rate of passage through the digestive system. The MRT is the average time that a food particle (or water molecule) takes to pass through the whole tract. An individual meal can be marked with both a particle marker (such as [103]Ruthenium Phenanthroline) and a fluid marker (such as [51]Chromium-EDTA). Collection of faeces at frequent intervals with analysis for the concentrations of the two markers makes it possible to calculate MRT as well as other parameters of rate of passage.

The MRT in macropodids fed on chopped lucerne hay is 11–14 hours for fluid digesta, but much longer (24–31 h) for particles (Hume & Dellow 1980). The MRT of two markers introduced into the hind stomach of wallabies is only 9 hours (Hume 1982), implying that the forestomach accounts for about two-thirds of the total MRT of particulate material. This is consistent with the forestomach as the main site of microbial fermentation in the macropodid digestive tract. It is, thus, the main site of production of the two main endproducts of gut microbial fermentation: volatile fatty acids (VFA), which are absorbed and utilised by the animal as its main source of oxidative energy, and microbial protein, an important source of amino acids. Most of the VFA are derived from plant cell wall material or fibre. Macropodids are able to digest 30–50% of the fibre in their diets of grasses, forbs and the leaves of shrubs.

In hind gut fermenters, the main site of digesta retention and microbial fermentation of fibre is the caecum and/or the colon. The stomach is always small and simple in structure. In wombats, which have only a vestigial caecum, the colon (Fig. 17.10d) is greatly expanded in both length and diameter and is haustrated so that particulate digesta are retained preferentially for 50–100 hours MRT (Hume 1982).

In the Greater Glider and ringtail possums the site of microbial fermentation is the caecum (Fig. 17.10f). This organ functions by preferentially retaining not the particulate digesta, but the fluid (and fine particles). The latter are fermented more easily. The coarser particles are eliminated from the gut as quickly as possible. In this way, these small marsupials, with their relatively high mass-specific nutrient requirements, are able to live on *Eucalyptus* foliage, a highly fibrous food source (Fig. 17.10f).

In terms of the digestive process, the Common Ringtail Possum, *Pseudocheirus peregrinus*, is remarkably similar to the rabbit. Selective retention of fluid and fine particles in the caecum is combined with caecotrophy, the ingestion of soft faeces of high nutritive value derived from caecal contents (Hume *et al*. 1984). This results in a long MRT for fluid (70 hours) compared with particulate digesta (54 hours) and the digestion of 45% of the fibre of eucalypt leaves.

In the Koala, the site of microbial fermentation is the caecum together with the proximal colon (Fig. 17.10g). The MRT of digesta is long (110 hours for particles and even longer, 251 hours for fluid digesta). Despite the slow rate of passage of digesta in the Koala, digestibility of fibre of eucalypt leaves is relatively low, about 25%, compared with ringtail possums.

Nutrient requirements

Energy. The basal metabolic rates (BMR) of marsupials lie below those of most eutherian mammals (see Respiration below). Their turnover rates of energy, protein and water also tend to be low (Hume 1982). These factors contribute to the ability of many marsupials to survive drought conditions.

Relatively few estimates have been made of the energy requirements of captive marsupials. The Common Wallaroo, *Macropus robustus erubescens*, requires 27% less digestible energy per day than do sheep (4.7 versus 6.5 $W/kg^{0.75}$). the Red Kangaroo, *Macropus rufus*, requires 20% less digestible energy for maintenance than do sheep (Hume 1974). Similarly, the digestible energy required for maintenance of captive Tasmanian Devils and Eastern Quolls is significantly less than that required by eutherian carnivores (Green & Eberhard 1979).

The energy cost of free existence, or field metabolic rate, depends very much more on the particular environment. Included are not only the energy costs of basal metabolism and activity associated with feeding and grooming (*ie* maintenance), but also those of thermoregulation, reproduction and foraging. Field metabolic rates have been found to range from 2.6 times BMR in the Koala to 5.8 times BMR in Leadbeater's Possum (Hume *et al*. 1984). In fact, marsupials are able to increase their metabolic rate up to 10–11 times BMR, so that their metabolic scope may surpass that of eutherians. For these reasons, it is inappropriate to make direct marsupial – eutherian comparisons of field metabolic rates.

Protein. Maintenance requirements for protein or nitrogen are little affected by ambient temperature or activity levels. Estimates derived from captive animals are thus directly applicable to animals in the wild.

With few exceptions, the maintenance nitrogen requirements of herbivorous marsupials are substantially below those of herbivorous Eutheria (Table 17.1). Two of the high marsupial values are from small wallabies from moist forest habitats (*Thylogale thetis* and *Macropus parma*). The lowest eutherian value is from an arid-adapted species, the African Rock Hyrax, *Procavia habessinica*. Maintenance nitrogen requirements are not determined wholly by phylogeny; habitat also plays a role.

Water. As might be expected, habitat type is important in determining water turnover rates, with species adapted to arid environments generally exhibiting lower rates of water turnover than species found only in moist forest habitats. In general, however, marsupials tend to have lower turnover rates than do eutherian mammals. Denny & Dawson (1975a) found that in five macropodid species held in the laboratory, the mean water turnover rate was 98 $ml/kg^{0.80}$/day. This compares with a mean of 134 $ml/kg^{0.80}$/day in seven eutherian species studied by Richmond, Langham & Trujillo (1962).

Table 17.1 Maintenance requirements of marsupial and placental herbivores for truly digestible nitrogen. (After Hume 1982; Hume *et al*. 1984; Robbins 1983a)

SPECIES	MAINTENANCE REQUIREMENT $(\text{mgN/kg}^{0}.75/\text{day})$
Marsupials	
Macropus robustus erubescens	160
Macropus robustus robustus	240
Macropus eugenii	230
Macropus giganteus	270
Trichosurus vulpecula	190
Phascolarctos cinereus	270
Aepyprymnus rufescens	200
Vombatus ursinus	210
Pseudocheirus peregrinus	290
Petauroides volans	560
Thylogale thetis	530
Macropus parma	480
Placentals	
Procavia habessinica	210
Equus caballus	380
Ovis aries	450
Cervus elaphus	680
Capreolus capreolus	410
Odocoileus virginianus	770

Vitamins and minerals. Studies on the Quokka on Rottnest Island suggest that this small wallaby's requirements for copper, cobalt and selenium are lower than those of sheep (Hume 1982). Whether this is true for other Macropodidae is not known. Koalas must also have low mineral requirements. The concentrations of phosphorus, sodium, zinc, selenium and copper in *Eucalyptus* foliage are often below the levels recommended for domestic sheep and horses. The same presumably holds for other strictly folivorous marsupials, such as *Petauroides* and *Pseudocheirus* species (gliders and possums).

Marsupials synthesise their own vitamin C (ascorbic acid) and so are independent of a dietary source of this vitamin. Requirements for B-vitamins and the fat-soluble vitamins A, D and K have not been established. Considerable work, however, has been done on vitamin E because of the susceptibility of several marsupials, particularly small wallabies, to vitamin E deficiency in captivity. It appears that stress associated with crowding in small enclosures increases the vitamin E requirement. The degenerative changes in the skeletal muscles, particularly of the hind limbs, can be reversed completely by oral dosing with vitamin E over several days.

Marsupials belong to a small group of animals, including the rabbit, in which nutritional muscular dystrophy is not prevented by trace amounts of selenium in the diet. In most other species selenium is an effective substitute for vitamin E.

CIRCULATORY SYSTEM

The circulatory system of marsupials does not differ markedly from that of the placentals or monotremes. It is, therefore, reasonable to suppose that the basic pattern must have been established early in mammalian evolution.

Heart

Some morphological differences exist between marsupial and placental hearts, but the difference in relative size of the hearts of the two groups is probably of greatest importance. The hearts of marsupials are about 30% heavier than eutherians of the same body mass (Table 17.2). Some unusual features of the marsupial heart have received comment in early work by Owen (1868) and in recent studies by Dowd (1969a, 1974). The right atrium is bifurcated in most marsupials, with one appendage of the auricle in front of and one behind the ascending aorta. The functional significance of this odd feature is obscure. The left atrium presents no peculiarities.

Table 17.2 Comparison of allometric equations relating cardio-respiratory variables to body mass in resting marsupials and placentals. (After Dawson 1983); (a)* normally accepted BMR values; (b)* minimum oxygen consumption values during experiments in which the cardiovascular measurements were made. Abbreviations: V_{O_2} = oxygen consumption; f_h = heart rate; V_s = heart stroke volume; V_b = cardiac output; f_r = respiratory rate; V_t = respiratory tidal volume; V_e = respiratory minute volume; M = body weight.

VARIABLE UNITS	MARSUPIAL	PLACENTAL	MARSUPIAL/ PLACENTAL
Vo2 (ml/min)			
(a)*	$7.10M^{0.75}$	$10.00M^{0.75}$	0.71
(b)*	$7.50M^{0.72}$	$11.60M^{0.76}$	$0.65M^{-0.04}$
f_h (min^{-1})	$116.00M^{-0.24}$	$241.00M^{-0.25}$	$0.48M^{0.01}$
V_s (ml)	$1.22M^{1.07}$	$0.78M^{1.06}$	$1.56M^{-0.01}$
V_b (ml/min)	$135.00M^{0.87}$	$187.00M^{0.81}$	$0.72M^{0.06}$
Heart mass (g)	$7.70M^{0.98}$	$5.80M^{0.98}$	1.33
f_r (min^{-1})	$22.10M^{-0.26}$	$53.30M^{-0.26}$	0.41
V_t (ml)	$12.10M^{0.98}$	$7.70M^{1.04}$	$1.57M^{-0.05}$
V_e (ml/min)	$267.00M^{0.72}$	$379.00M^{0.80}$	$0.72M^{-0.08}$

Vascular System

Several other aspects of the vascular system merit comment. The origin of the arteries arising from the aortic arch shows as much variation in marsupials as exists throughout the entire range of the Eutheria (Pearson 1940).

The vascular organisation of the metatherian brain has been described in various species (*Didelphis* – Dom, Fisher & Martin 1970; Voris 1928b; Wislocki & Campbell 1937; *Macropus rufogriseus* – Craigie 1938; various other Australian species – Sunderland 1941). In all species examined, the arteries penetrating the brain and central nervous system terminate in non-anastomosing capillary loops instead of communicating with the venous branches through an interconnected capillary network as found in other mammals (Swindle 1937; Wislocki & Campbell 1937; Sunderland 1941).

Tissue is supplied with blood by several loops which interdigitate, but do not unite. The function of the loop has not been investigated, but it is possible that this arrangement could reduce damage due to oxygen lack in the event of blockage.

The blood supply to the testes in Metatheria is also unusual (Harrison 1948, 1949). With the exception of the marsupial moles, the testicular artery in the stalk of the scrotum divides into 50 to 154 separate vessels, which then spread over the surface of the testes. The testicular veins form a similar arrangement

and, as they pass up the spermatic cord in close apposition to the arteries, a rete mirabile is formed. From functional studies in a few species (Setchell & Waites 1969; Waites 1970; Setchell 1977), there is compelling evidence that, like the eutherian pampiniform plexus, the rete mirabile provides a mechanism for countercurrent heat exchange to regulate the temperature of the scrotal contents below normal body temperature (Setchell 1977; also see Chapter 29). In addition to a thermoregulatory function, the rete mirabile also appears to be able to eliminate testicular arterial pulse without significantly changing mean blood pressure, although the functional importance of this is not yet clear (Setchell & Waites 1969).

Beneath the skin of the forelimbs of the large kangaroos is a dense superficial network of veins (Needham, Dawson & Hales 1974). The area covered by this network also corresponds to the area licked by the kangaroos when they are subjected to heat stress. Forelimb blood flow also increases greatly under these conditions, demonstrating a site of significant heat transfer (Fig. 17.11). That the large tail of kangaroos might also have vascular arrangements conducive to regional heat transfer has often been considered, and there is some evidence in support of this idea (Young & Webster 1974; Needham & Dawson 1984).

Figure 17.11 Posture of a desert kangaroo in sparse shade on a hot summer day. Licking of the vascularised region of the forearms helps heat loss. Tail is pulled between the legs to reduce radiant heat inflow; blood flow to the skin of the tail is reduced in these conditions. (After Dawson 1983; © ABRS)   [F. Knight]

General aspects of marsupial cardiovascular function

Much of the difficulty in quantifying physiological differences between marsupials and eutherians arises because of the effect of body size. Relationships often exist between anatomical and physiological variables and body mass, but these are non-linear. They may be able to be described, however, by allometric (that is, non-linear) equations. Such equations have the form $y = a\mathrm{M}^b$, where y is a physiological or anatomical variable which is a function of body mass (M in kg) raised to an exponent b. In logarithmic form these equations give a linear function, $\log y = \log a + b \log \mathrm{M}$. The constant a, (y-intercept) appears to be characteristic for different phylogenetic groups, while b, the mass exponent or the slope of the line in a logarithmic graph, appears constant for a particular variable, even between animal groups.

The allometric equations for the resting heart rates of marsupials and eutherians have similar exponents, -0.26, but the y-intercept levels are very different. The y-intercept in marsupials was found to be less than half that in eutherians (Kinnear & Brown 1967). The low oxygen consumption found for marsupials (Dawson & Hulbert 1970) did not account fully for this difference and thus prompted further investigations into the cardiovascular and respiratory systems

of marsupials (Dawson & Needham 1981). The results of these studies are summarised in Table 17.2 and take the form of a series of allometric equations for different cardiovascular and respiratory variables.

The organisation of the cardiovascular system of resting marsupials differs from that of eutherians in two ways (Table 17.2). Firstly, the transport of oxygen from the lungs to the tissues, as measured by cardiac output (V_b), generally parallels the difference in the basal oxygen consumption. Secondly, the low resting heart rate of marsupials is lower than would be anticipated from the differences in minimal oxygen consumption. It seems that the hearts of marsupials are larger than those of placentals and pump more blood per beat by effecting larger stroke volumes. The maximum heart rates of marsupials and eutherians are similar (Baudinette 1978). Since heart stroke volume remains relatively constant during exercise (Baudinette, Seymour & Orbach 1978), marsupials, with their larger stroke volumes, probably have the potential for a greater cardiac output. This seems surprising for a group of mammals often regarded as primitive in their metabolic abilities. Marsupials, however, do have a high metabolic capability (Dawson & Dawson 1982).

RESPIRATION

Metabolic relationships of marsupials

The level of activity of the cellular metabolic processes is assessed from measurements of oxygen consumption. The basal metabolic rate (BMR) is often considered to provide an indication of underlying metabolic capabilities. The BMR of the various groups of mammals and birds can be compared using allometric equations (Table 17.3). Among the homeotherms, the passerine or perching birds seem to have the greatest metabolic capability, while marsupials seem to fall well below the eutherians in metabolic ability, but this is not actually the case, as shall be demonstrated below. Resting body temperatures of marsupials also are lower than those of the eutherians, 2–3°C on the average (Table 17.3). Contrary to earlier expectations, raising the body temperature of marsupials does not bring the BMR up to eutherian levels.

Metabolic responses to cold

There are two aspects of thermoregulation in homeotherms: the production of sufficient heat to maintain body temperature in cold conditions and the loss of excess heat in hot conditions. Enhanced heat production is generally assumed to have evolved first. The first mammals were very small insectivorous forms and their heat producing abilities enabled them to occupy the cool, nocturnal, insectivorous niche while the reptiles were active during the day. Many small mammals, including many marsupials, occupy this niche today and are still faced with the same basic thermoregulatory problem, that is, a high rate of heat loss. This is due to their relatively large surface area compared to the body mass, the volume of heat producing tissue, and the limits on the insulation that a small mammal can carry. The maintenance of body temperature in these circumstances obviously requires an equivalent level of heat production by small mammals. Marsupials, with their low BMR, might have been expected to have thermoregulatory difficulties.

Recent studies have shown, however, that marsupials are able to markedly increase metabolism 10 to 11 times. Their absolute summit metabolism may surpass that of eutherians (Dawson & Dawson 1982; Smith & Dawson 1985). The larger expansibility of metabolism in marsupials corresponds with the flexibility in their cardiovascular system and lung functions.

Table 17.3 Average resting body temperature and basal metabolism of some amniote vertebrates. (After Hulbert 1980)

ANIMAL GROUP	BODY TEMPERATURE (°C)	BASAL METABOLISM (watts per $kg^{0.75}$)
Reptiles		
Lizards	30.0	0.40
Snakes	30.0	0.48
Monotremes		
Echidnas	31.5	0.92
Platypus	32.1	2.21
Marsupials	35.5	2.35
Placentals		
Edentates	33.0	2.66
Advanced	38.0	3.34
Birds		
Nonpasserine	39.5	4.02
Passerine	40.5	6.92

Torpor in marsupials

Torpor, particularly short term or daily torpor, is widespread among small marsupials (Dawson 1983). Apparently, torpor is used for energy conservation, since food restriction is often necessary to bring about torpor in laboratory conditions. Torpor is not a switching off of the thermoregulation system, as was previously thought, but is a well-controlled thermoregulatory process. Many of the small marsupials only allow body temperature to drop to 15 to 17°C, even if air temperature falls lower. Some marsupials do show a pattern of longer term torpor, much like the seasonal hibernation of eutherians. The pygmy-possums (Burramyidae) show this pattern and allow their body temperatures to drop to much lower levels.

Marsupial torpor differs from that of eutherians in the characteristics of arousal. Whereas eutherians rely on brown fat, a special heat producing tissue, to accelerate rewarming on arousal, marsupials do not appear to have this tissue and the mechanism of their arousal is not understood.

Lung function and gas exchange

Early anatomists (for example, Owen 1868) pointed to minor differences between marsupials and eutherians as regards lung morphology. Detailed studies using modern techniques are lacking. The functional differences seem to follow the pattern seen in heart function. Dawson & Needham (1981) suggested that in common with heart rates, the resting respiration rates of marsupials are less than half those of eutherians (Table 17.2). Large tidal volumes are associated with these low respiratory frequencies. The net effect is that the allometric equation for minute volume of marsupials bears the same relationship to the minute volume of eutherians as do the respective resting oxygen consumptions (Table 17.2). Values for respiratory variables derived from these equations are similar to those obtained for two marsupials in a study by Nicol & Maskrey (1977).

Other roles of the respiratory system

Active evaporative cooling to aid heat loss in mammals takes three forms: panting, sweating and licking. Marsupials utilise all three forms (Dawson, Robertshaw & Taylor 1974; Dawson 1984), but panting, the rapid movement of air in and out of the respiratory tract, is most common. Panting has the advantage that the rate of air movement over the evaporating surfaces, the nasal mucosa and upper respiratory tract, can be finely controlled and adjusted to the heat loss requirements. Sweating does not have this advantage. The rapid ventilation of the respiratory system can cause an excess loss of CO_2, which may upset the pH balance of the blood. The Long-nosed Potoroo, *Potorous tridactylus*, and the Eastern Barred Bandicoot, *Perameles gunnii*, are capable of increasing respiratory minute volume (Ve) 26 and 16 times, respectively (Nicol & Maskrey 1977). To reduce the impact of this on blood pH, ventilation increases were restricted to the upper regions of the respiratory tract, thereby limiting the increase in alveolar ventilation.

EXCRETION

Nature and distribution of body water

The amount of water in the body of marsupials is similar to that found in eutherians. Values range from 72.5%–78%, or 725–780 ml H_2O/kg body weight, for the large kangaroos, *Macropus giganteus*, *M. robustus* and *M. rufus*, to about 60% for the small Tammar Wallaby, *M. eugenii* and the Long-nosed Potoroo, *Potorous tridactylus* (Denny & Dawson 1975a). Values within this range have been found for other marsupials, such as large dasyurids (Green & Eberhard 1979), bandicoots (Hulbert & Dawson 1974c) and a variety of other macropodids (Bakker & Main 1980).

The reasons for the variability in water content are several. The kangaroos have large fermentation chambers in their alimentary systems which can contain water equivalent to 12 to 13% of body weight. This accounts for the high values in large kangaroos relative to the smaller species with more simple guts (Denny & Dawson 1975a). Body fat contains much less water than other tissues (such as muscle) and when large variations occur in fat deposits, the proportion of water within the body changes markedly (Hulbert & Gordon 1972; Bakker & Main 1980). A seasonal variation between 59% and 75% in the body water content of bandicoots has been recorded (Hulbert & Gordon 1972).

Several marsupials can easily tolerate a loss of about 30% of their total body water during dehydration. In such circumstances body solids are lost along with the water and the percentage of water tends to be unchanged (Hulbert & Dawson 1974c; Denny & Dawson 1975b). The nature of this loss of solids is poorly understood. It may be related to depressed food intake, so that gut fill is reduced and metabolism of body reserves such as fat and protein occurs.

Body water is contained within a number of compartments. Most of the water is intracellular. Extracellular water is generally divided into plasma water (in the vascular system) and interstitial water. The latter occupies an extravascular space between and surrounding all cells and tissues. Gut water may be considered as contained within a third compartment. The contents of these fluid compartments are not static but in dynamic equilibrium; in some circumstances, such as dehydration, considerable variation occurs. A comprehensive study dealing with this aspect of the physiology of arid zone kangaroos was carried out by Denny & Dawson (1975b).

The composition of the body fluids of marsupials does not differ markedly from that of other mammals. Generally, studies have examined only the plasma constituents and their variability. Early studies were summarised by Tyndale-Biscoe (1973). Recent studies dealing with aspects of electrolyte balance have been made by Reid & McDonald (1968b), Wilson & Hoskins (1975), Denny & Dawson (1977), Green & Eberhard (1979), Hume & Dunning (1979) and Bakker, Bradshaw, & Main (1982).

Kidney structure and function

As in other mammals, the responsibility for maintaining proper fluid balance and composition in Metatheria largely belongs to the kidneys. While some salts, water and metabolites are lost via other routes, the composition of the body fluids is determined more by what the kidneys retain than by what is taken in through the mouth. The importance of the kidney is shown by calculations using the data of Denny & Dawson (1975a, 1975b, 1977). For a 23 kg Red Kangaroo, the total body water of 17 litres is filtered by the kidney glomeruli about 17 times a day. The total blood volume is pumped through the kidneys over 200 times in the same period.

The first detailed studies of marsupial kidneys using modern techniques (Pak Poy 1957; Reid & McDonald 1968b) confirmed the earliest work, reported in Owen (1868), that in gross structure and function the kidneys were typically mammalian. According to Sperber's 1944 classification, the kidneys are simple, with a single papilla. Sperber considered this type to be primitive but this would appear to reflect a phylogenetic prejudice.

The Common Brushtail Possum, *Trichosurus vulpecula*, has typical metatherian kidneys (Reid & McDonald 1968b). The junction between the cortex and medulla is well defined and the latter is divided into an inner and outer zone. There is a single low papilla projecting into the pelvis where the collecting ducts open. There are two types of nephron in *T. vulpecula*, cortical and juxtamedullary. Cortical nephrons have short loops of Henle which turn in the cortex. Juxtamedullary nephrons have glomeruli near the cortical-medullary boundary and long loops of Henle which descend into the medulla, sometimes almost to the papilla. With their long loops, the juxtamedullary nephrons act in concert with the medullary blood vessels, the vasae rectae, to produce a concentrated urine by a counter-current mechanism. The vasae rectae occur as discrete bundles of straight vessels descending deep into the medulla in a course parallel to the loops of Henle, where they turn sharply and return to the outer zone of the medulla to drain into the venous system (Reid & McDonald 1968b).

Differences in kidney structure have been noted between species of marsupials. The kidneys of the Red Kangaroo, for example, contain more glomeruli than those of the Common Wallaroo (Denny & Dawson 1977). This explains the observed larger glomerular filtration rate and the greater percentage of plasma filtered per transit of the kidney in the former species.

Glomerular structure may influence the function of the kidney, but the morphological aspect attracting most interest has been the relative medullary length. Sperber (1944) reported variations in the renal morphology of mammals which occupy different habitats. Further, Schmidt-Nielsen & O'Dell (1961) demonstrated that the increasing ability to concentrate urine is correlated with the relative thickness of the medulla, which roughly approximates the length of the juxtamedullary nephrons. Data from marsupials from differing environments are given in Table 17.4, supporting the view that marsupials from more water restricted environments have a larger relative medullary length and conserve water by producing a more concentrated urine. Much is yet to be discovered about the kidney function of marsupials since even their maximum capacity is

not known. The Kultarr, *Antechinomys laniger*, a small dasyurid from central Australia, has been reported to have the highest relative medullary length of any mammal, 8.0 (Sperber 1944), but its ability to concentrate urine is not known.

Table 17.4 Relative medullary thickness of the kidneys and osmotic concentrations of the urine of some marsupials. *These estimates are based on the assumption that urine osmotic pressure equals 2 (electrolyte concentration) + urea concentration. (MacMillen & Lee 1967)

SPECIES	RELATIVE MEDULLARY THICKNESS	URINE OSMOLARITY (mosmol/L)			REFERENCE
		Water ad lib.	Water restricted		
		(mean)	(mean)	(maximum)	
Sminthopsis crassicaudata		2 149	2 322	3 519	Morton 1980a
Planigale maculata		2 514	2 317	2 951	Morton 1980a
Dasycercus cristicauda			2 840*	3 958*	Schmidt-Nielsen & Newsome1962
Perameles nasuta	5.9	2 110	3 512	4 175	Hulbert & Dawson 1974c
Macrotis lagotis	5.9	3 075	3 566	3 976	Hulbert & Dawson 1974c
Isoodon macrourus	5.3	1 985	2 942	3 126	Hulbert & Dawson 1974c
Echymipera rufescens	4.5	1 465			Hulbert & Dawson 1974c
Macropus rufa	5.8	1 460	3 135	4 054	Denny & Dawson 1977
Macropus robustus	7.2	935	2 840	3 270	Denny & Dawson *1977*
Marcropus eugenii	5.9	1 862	3 094	3 231	Purohit 1971
Phascolarctos cinereus	3.0	1 212	1 691	1 843	Degabriele *et al*. 1978

The kidneys play an important and complex role in the excretion of nitrogenous wastes. Certain nitrogenous materials such as creatinine are lost by the kidney at a more or less constant rate depending on the body weight and basal metabolism (Frazer & Kinnaer 1969). Urea, the principal nitrogenous excretory product of mammals, has a variable pattern of excretion. Amino acids cannot be stored in the body. Those in excess of requirements for body maintenance, growth or reproduction are broken down in the liver. The amino groups are converted via ammonia to urea and usually excreted.

In carnivorous and some omnivorous mammals, urea is a major component of the excretory load and problems may arise with the supply of water for its excretion. Herbivorous marsupials which live on good quality pasture, that is, high in protein, face a similar situation. On dry grass, however, animals may be deficient in protein and an attempt may be made to conserve the urea and use it to elaborate more protein. Such marsupials rely on the metabolic capabilities of gut microorganisms (bacteria and protozoa) to synthesise new protein from non-protein nitrogen. This recycling of urea takes place, together with the digestion of plant fibre, in the expanded fermentation chambers of the gut. These chambers are in the foregut of the macropodids and the hind gut of the phalangers, wombats and the Koala (see Feeding and Digestion above). In the case of the macropodids, the urea may enter the foregut by way of saliva or

simply by diffusion across the foregut wall (Tyndale-Biscoe 1973). The advantages of this process to a marsupial on low nitrogen food would be very significant.

Active urea retention by macropodid marsupials could also be important in reducing water loss when this commodity is scarce (Ealey 1967), but studies on the Tammar Wallaby (Barker 1971) do not seem to support this hypothesis. The Common Wallaroo and the Red Kangaroo treat urea similarly when they are hydrated and on an adequate diet. Approximately 70% of filtered urea is reabsorbed from the kidney filtrate. During dehydration, the pattern does not change for the Red Kangaroo, but the Common Wallaroo resorbs about 90% of the filtered urea and plasma urea concentration increases substantially. In dehydrated Red Kangaroos, urea resorption is independent of urine concentration, but in the Common Wallaroo, the urea urine to plasma ratios remains constant, suggesting that urea resorption is a passive process, related only to the increase in water resorption in the kidney. The Common Wallaroo does, nevertheless, tend to retain urea and have a lower nitrogen requirement (Denny & Dawson 1977).

Excretion via faeces

The gastrointestinal tract also regulates both water and salt losses. Balance studies on several marsupials show that more water may be lost via this route than via the kidney (Barker 1971; Hulbert & Dawson 1974c; Degabriele, Harrop & Dawson 1978). In bandicoots from differing environments, faecal water loss always exceeds urinary water loss except in the well-hydrated Bilby, *Macrotis lagotis* (Hulbert & Dawson 1974c). Presumably, this arid zone species normally does not have free water available under natural conditions.

SENSE ORGANS AND NERVOUS SYSTEM

In metatherians, as in most other vertebrates, aggregates of specialised receptor cells which are usually derived from ectoderm form the various characteristic sensory organs (for example, the eye, cochlea, vomeronasal organ) which are linked by special afferent neural pathways to the central nervous system. Marsupials, in general, possess the standard array of sensory organs including a variety of cutaneous receptors. Most of these sensory units are similar to those described in eutherian mammals and vary, if at all, only in minor structural and functional details (Barbour 1977; Johnson 1977; Gates & Aitken 1984).

Sensory organs

Visual system. The metatherian eye is a large and prominent structure. Exceptions are the marsupial moles *Notoryctes* species and the caenolestid marsupials of South America. Although its morphology has received little attention, it appears to conform closely in general morphology and development to the eutherian eye.

The retina comprises typical layers of amacrine, bipolar and horizontal cells with the rod and cone receptor cells forming the outermost layer (Johnson 1977). As in many nocturnal eutherians, several marsupial species possess a tapetum lucidum, a reflective layer of cells around the external surface of the retina which is thought to reflect light back on to the receptor cell layer and thus increase the sensitivity of photoreception at low levels of illumination. This layer appears to be particularly well developed in the Virginia Opossum *Didelphis virginiana* (Walls 1939).

The retinal cone cells of marsupials are often double and contain either non-pigmented (O'Day 1938) or pigmented oil droplets (Hoffman 1877). These oil droplets have not been seen in cone cells of eutherians, but are a common feature of reptiles, birds and prototherians, (Griffiths this volume; Walls 1939; Johnson 1977). Their function remains a matter for speculation.

Photoreceptive messages pass from the receptor layer to the ganglion cell layer and are transmitted via the optic nerve and chiasma to ipsilateral and contralateral areas in the geniculate nuclei, pretectum, superior colliculus, suprachiasmatic nucleus and to the accessory optic tract of the midbrain tectum (Lent & Rocha-Miranda 1974; Johnson 1977). A well-developed visual streak and area centralis are present in the Tasmanian Pademelon, *Thylogale billardierii*, the Tammar Wallaby, *Macropus eugenii* and the Tasmanian Devil, *Sarcophilus harrisii* (Tancred 1981). These features are less developed in the retina of bandicoots, *Isoodon* species. In the Southern Hairy-nosed Wombat, *Lasiorhinus latifrons*, the area centralis is absent, although the visual streak is prominent.

The retinal projections to various regions in the brain have been examined in a few marsupial species: the Common Ringtail Possum (Pearson, Sanderson & Wells 1976); the Southern Hairy-nosed Wombat (Sanderson & Pearson 1981); and the Tasmanian Devil (Sanderson, Pearson & Haight 1979). In general, the pattern of input is equivalent in each species examined, with retinal fibre terminations in seven regions of the brain: dorsal and lateral geniculate nuclei, lateral posterior nucleus, pretectum and superior colliculus, suprachiasmatic nucleus of hypothalamus and the accessory optic system. In Brush-tail Possums, following mid-saggital transection of the optic chiasma, monocular occlusion and conditioning, there is still a high degree of interocular transfer of information on all behavioural tasks, suggesting a pathway available for mediating this transfer of visual information (Robinson 1982).

Retinal projections to the dorsal lateral geniculate nucleus form a complex, pronounced lamination of cells and fibres (Johnson & Marsh 1969; Pearson *et al*. 1976; Sanderson & Pearson 1981). In most species, the accessory optic system and lateral posterior nucleus receive contralateral retinal projections whereas the other areas receive bilateral inputs. In the Southern Hairy-nosed Wombat (Sanderson & Pearson 1981), however, the accessory optic system receives bilateral projections from the retina and has considerable overlap of fibres from both eyes to the superior colliculus. Also in this species, the monocular segment of the dorsal lateral geniculate nucleus is twice that of the binocular segment, reflecting perhaps the lateral position of the eyes which have a large lateral monocular field and small frontal binocular field of vision (Sanderson & Pearson 1981). The cytoarchitecture of the retinal projection to the lateral geniculate nucleus in the Tasmanian Devil is simpler than any other marsupial examined so far and the monocular segment of the projection accounts for a massive 40% of the nucleus, which is more extensive than in any other polyprotodont marsupial. The cytoarchitecture and retinal projections of macropodid species vary from simple in *Bettongia* species to complex in the larger Tammar Wallaby and the Eastern Grey Kangaroo, *Macropus giganteus*, where bilateral retinal projections are found within the same lamina of the dorsal lateral geniculate nucleus (Sanderson, Haight & Pettigrew 1984).

The marsupial moles, like their eutherian counterparts, have very poorly developed eyes and visual system (Sweet 1906). In contrast to eutherian moles, all remnants of the retinal photoreceptor and ganglion cells, optic nerves and the cranial nerves which normally innervate eye musculature are lacking (see Chapter 23).

Vestibular system.Very little is known about this system in the Metatheria, but the few observations which have been made revealed no specific differences in structure or function from those of eutherian mammals (Voris & Hoerr 1932; Larsell, McCrady & Zimmerman 1935; Johnson 1977).

Audition and the auditory system. With the exception of the Virginia Opossum (McCrady, Wever & Bray 1937; Lende 1963a; Ravizza, Heffner & Masterton 1969) and the Common Brushtail Possum (Aitken, Gates & Kenyon 1979; Gates & Aitken 1984) the structure and function of this system have largely been ignored.

Efficient reception of sound is important for most marsupials because of their propensity for nocturnal activity and the importance of sounds in the social organisation and intraspecific interaction of most species (Eisenberg, Collins & Wemmer 1975; Biggins 1984). Most marsupials have large or relatively large, mobile pinnae which are highly efficient locators and collectors of environmental sound waves. External pinnae are very large in the Bilby, *Macrotis lagotis*, and, at the other extreme, are completely absent in the fossorial Marsupial Mole *Notoryctes typhlops*, where reception and location of airborne sounds are apparently not of great importance.

The shape and arrangement of the middle ear ossicles in a variety of marsupials are described by Secal (1969, 1970) and used to draw conclusions about the phylogeny of marsupials. Doran (1879) suggests that the shape of the stapes in the Phalangeridae, and, in fact, most marsupial species, is intermediate between the stirrup-like eutherian stapes and the columelliform stapes of the Prototheria (see Tachyglossidae Chapter 15).

Little is known about cochlear structure and function in marsupials. In the Virginia Opossum, there is a close correlation between development of the cochlea and auditory sensitivity in pouch young (McCrady *et al*. 1937; Larsell, McCrady & Larsell 1944). Frequency perception is strikingly related to cochlear development in this species. Perception of middle range frequencies by pouch young coincides with development of the middle section of the cochlear coil whereas response to high and low frequencies occurs following maturation of apical and basal segments of the coil.

The structure of the cochlea in adult metatherians seems to have been studied only in the Common Brushtail Possum (Aitken *et al*. 1979) which, perhaps not surprisingly, shows considerable similarities with the eutherian cochlea. In Brushtail Possums, the cochlea consists of a 17 mm long, 3.5 turn coil, which is deeply embedded in the temporal bone. The organ of Corti comprises three rows of outer hair cells and a single row of inner hairs arranged in an eutherian configuration (Aitken *et al*. 1979). Sound reception and transduction by the cochlea results in signals being relayed to the ventral cochlear nucleus by the acoustic branch of the auditory nerve and thence to the dorsal cochlear nucleus which lies at the base of the inferior cerebellar peduncle (*Didelphis* – Stokes 1912; *Macropus rufus* – Cowley 1973; *Trichosurus* – Aitken & Kenyon 1981).

Neural pathways from the cochlear nuclear complex to the auditory midbrain regions are described (Stokes 1912; Cowley 1973; Johnson 1977; Aitkin & Kenyon 1981; Gates & Aitkin 1984; Aitkin, Byers & Nelson 1986a; Aitkin *et al*. 1986b). In general, the nature of projections to the auditory midbrain and their functional significance are thought to resemble those of eutherians.

Electrophysiological studies of the inferior colliculus of Brushtail Possums, which is similar in structure to that of *Didelphis* (Huber & Crosby 1943) and also the Cat (Berman 1968; Aitkin & Kenyon 1981), showed a wide range of frequency responses (<1.0 kHz–30 kHz) which closely resembled a behavioural-base frequency range established for *Didelphis* (Ravissa *et al*. 1969). Subsequent observations (Aitkin, Gates & Phillips 1984) demonstrated a precise spatial tuning of binaural units in the inferior colliculus of Brushtail

Possums to high frequency sounds and white noise. White noise, however, was in general far more effective in evoking spatial tuning than pure tones; an interesting observation since most of the social vocalisations of Brushtail Possums have a broad frequency base.

From the inferior colliculus, auditory neural pathways project to the medial geniculate nucleus of the thalamus (Stokes 1912; Rockel, Heath & Jones 1972; Aitkin & Gates 1983) and terminate within the auditory cortex which lies lateral and ventral to the sulcus of the temporal cortex. These afferent fibres arise ipsilaterally from medial and suprageniculate nuclei, also contralaterally from corresponding regions in the cortex by way of the anterior commissure and, in diprotodont marsupials like Brushtail Possums (but not in *Didelphis*), the fasciculus aberrans (see Nervous System, this Chapter, for structural relationships). In *Didelphis*, midbrain auditory projections also apparently terminate in the putamen, globus pallidus and lateral amygdaloid nuclei of the basal ganglia. Unlike most eutherians, one auditory field rather than multiple fields, has been found in the primary auditory cortex in Brushtail Possums (Gates & Aitkin 1984). An orderly tonotopic sequence was identified in which high frequencies were located dorsally and low frequencies ventrally, a spatial arrangement not found in eutherian mammals.

Chemoreception

Olfactory organs and systems. Marsupials have evolved a large array of odour-producing cutaneous glands which are important for social communication (Biggins 1984; Russell 1985). Not surprisingly, perhaps, the olfactory system is well developed. There have been few detailed studies of the olfactory organs and their neural pathways in the central nervous system in metatherian species (Herrick 1924; Phillips & Michels 1964; Switzer 1973; Kratzing 1978; Biggins 1979; see also recent reviews by Johnson 1977; Russell 1985).

In marsupials, as in most mammals, two sensory organs, the typical olfactory epithelium and the vomeronasal (or Jacobson's) organ, are responsible for olfaction. The olfactory epithelium is extensive in those species which have been examined and the morphology of receptor cells in this epithelium appears similar to that of other mammals (Parsons 1971; Kratzing 1978, 1984b; Biggins 1979). In the Northern Brown Bandicoot, *Isoodon macrourus*, (Kratzing 1978, 1984b and the Common Brushtail Possum, *Trichosurus vulpecula* (Biggins 1979), olfactory epithelium covers the ethmoturbinate and extends into the maxillary sinuses forming a limited dorsal region of olfactory tissue within these sinuses.

The vomeronasal organ provides an additional region of sensory epithelium in the nasal cavity and is prominent in all marsupials examined (Broom 1896b; Kratzing 1984b) and particularly extensive in the Honey Possum, *Tarsipes rostratus* (Kratzing 1984b). The sensory epithelium lining the vomeronasal organ is responsive to odours (Tucker 1963) and similar in structure to olfactory epithelium, except that its 'axon-sending cells' appear to be unciliated (Andres 1970). This organ is located bilaterally in the anterior region of the nasal cavity in a tubular structure at the base of the nasal septum. The function of the vomeronasal organ is still controversial, but it appears to be primarily an organ of chemoreception which may be stimulated by low volatility compounds unable to reach and stimulate the olfactory epithelium (Wysocki, Wellington & Beauchamp 1980; Russell 1985). It is important in sexual behaviour of mammals (Powers & Winans 1975) and is believed to be a receptor for secreted sex hormones which can provide information on reproductive status (Estes 1972).

Separate neural pathways transmit information from these two olfactory organs to the brain (Johnson 1977). Sensory afferents from the olfactory epithelium are received by the olfactory bulbs, which are similar in morphology to their eutherian counterparts and are very prominent structures in marsupials, accounting for half of the forebrain in some species (Johnson 1977). Olfactory bulb anatomy was described in detail for *Didelphis* (Herrick 1924), and Phillips & Michels (1964) provided some evidence for bulbar regional specialisation. Efferent pathways from the olfactory bulbs were described by Johnson (1977).

Efferents from the vomeronasal organ form the vomeronasal nerve which terminates in the accessory olfactory bulb, an independent structure on the antero-dorsal surface of the olfactory bulb. Efferent fibres from the accessory bulb project to the bed nucleus of the stria terminalis and to the medial and cortical amygdaloid nuclei (Scalia & Winans 1975).

Taste. Tongue structure in relation to the morphology and distribution of gustatory (taste) elements has not been studied extensively, with the exception of *Didelphis* (Krause & Cutts 1982). Three prominent vallate papillae are present in all species examined, (Poulton 1883; Parsons 1896; Osgood 1921; Jones 1949; Krause & Cutts 1982) and compound filiform papillae are distributed widely across the dorsum of the tongue.

Tactile receptors. As with taste, there is little information on tactile receptors in marsupials. Tactile sensory hair follicles have been described in the Virginia Opossum (Mann 1968) which resemble, in structure, those of eutherians. Meissner's corpuscles occur in the hand skin of *Didelphis* and the Red Kangaroo (Winkelmann 1964) in association with other types of mammalian sensory nerve endings. Hollis & Lyne (1974) examined the innervation of mystacial vibrissa follicles in the Common Brushtail Possum and found that each follicle capsule received one to five trunk nerves containing up to 500 myelinated fibres. They described four types of nerve endings in the follicles including Merkel cells with associated neurite complexes in the outer layers of epithelial cells.

The apparent importance of tactile communication in social behaviour of marsupials (Biggins 1984) suggests that future studies may show a wider and more complex distribution of tactile receptors in the Metatheria.

Nervous System

The central nervous system of marsupials has been studied in more depth than most other metatherian systems. Little attention, however, has been given to the peripheral and autonomic components. Most of the impetus for these studies, in particular those made before 1970, was the assumption that the brains of metatherian mammals would reflect inferior stages in mammalian evolution. Although this precept is now widely regarded as inappropriate, the detailed understanding it generated on the structure and function of the metatherian central nervous system is its lasting epitaph.

Because of its presupposed primitive evolutionary status and its availability for research, the Virginia Opossum received considerably more attention in the past than did other marsupials. There is now also an increasing body of knowledge on other marsupial species, the Common Brushtail Possum in particular. The structure and function of the metatherian nervous system is very adequately reviewed by Tyndale-Biscoe (1973), Barbour (1977) and, especially, Johnson (1977) and the reader is referred to these detailed accounts for specific information. Emphasis will be given here to the similarities and differences which exist between metatherian and eutherian nervous systems and to data from some recent functional and developmental studies.

With a few exceptions (see below) the central nervous systems of metatherian (Fig. 17.12a) and eutherian mammals are remarkably similar in structure and, where information is available, function. Similarities in the neural pathways and projections of the special sensory systems of marsupials have been described above.

The spinal cord in marsupials is equivalent in its organisation to eutherian mammals, with a relatively undistorted arrangement of sensory, internuncial and motor cell columns and a typical pattern of laminations within these cell columns. Some minor differences, however, have been reported. For example, the terminal area and Lamina VI, which probably contain internuncial cell columns with connections between other adjacent columns, are larger in eutherians than marsupials (Rees & Hore 1970), perhaps reflecting a great cortical involvement in the coordination of spinal cord activity in eutherians. Spinal cord enlargements occur in areas of increased input and output, especially the segments involved in fore- and hind limb innervation, as in eutherian species. The organisation and distribution of efferent motor fibres in the ventral spinal roots and afferent sensory fibres in the dorsal roots are also similar (Oswaldo-Cruz, Pagani & Rocha- Miranda 1965; Rocha-Miranda & Oswaldo- Cruz 1965). Descending neural pathways in the spinal cord, such as
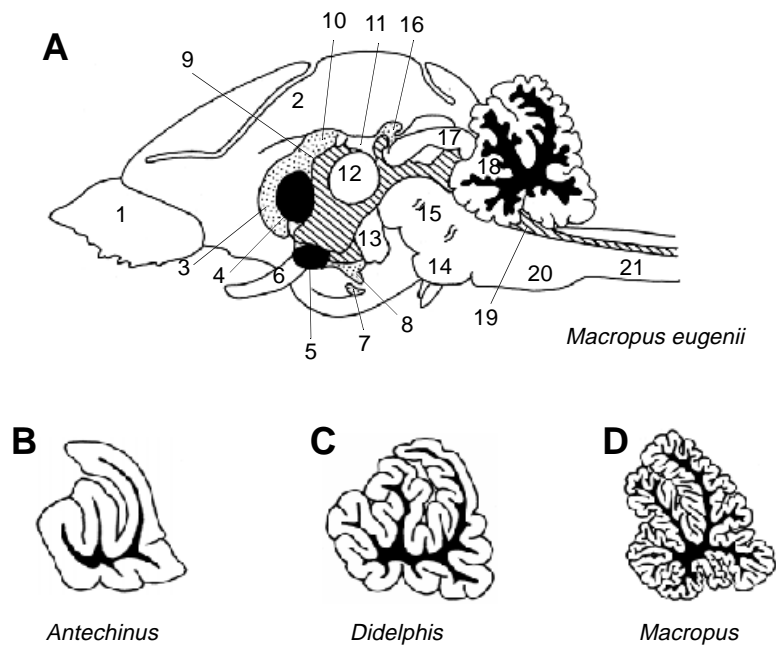
Figure 17.12 A, Sagittal section through the brain of a diprotodont marsupial the Tammar Wallaby (*Macropus eugenii*) showing the organisation and relationship of midline structures. **B–-D**, Medial sagittal sections through the vermis of the cerebellum of three marsupial species, showing increasing degrees of development of the cerebellar cortex, from simple (*Antechinus*) to complex (*Macropus*), with increasing body size. Similar sequences of increasing cortical complexity also occur in the cerebellum of eutherian mammals (Johnson 1977). B, a marsupial mouse, the Yellow-footed Antechinus (*Antechinus flavipes*); C, the American Virginia Opossum (*Didelphis virginiana*); D, the Red Kangaroo (*Macropus rufus*). 1, olfactory bulb; 2, cerebrum; 3, hippocampal commissure; 4, anterior commissure; 5, optic chiasm; 6, optic nerve; 7, pituitary; 8, hypothalamus; 9, 3rd ventricle; 10, fornix; 11, habenula; 12, interthalamic adhesion; 13, mamillary body; 14, pons; 15, cerebral peduncle; 16, pineal; 17, mesencephalic tectum; 18, cerebellum; 19, 4th ventricle; 20, medulla oblongata; 21, spinal cord with central canal. (A, after Renfree *et al.* 1982; B–D, after Johnson 1977; © ABRS)   [B. Scott]

the rubrospinal tract and reticulospinal fibres (which are thought to be involved in motor control and extend throughout the cord), also closely resemble their eutherian counterparts (Martin & Dom 1970, 1971).

Direct projections of the spinal cord onto the cerebellar cortex have been observed in Brushtail Possums (Watson *et al*. 1976). These and similar studies in *Didelphis* (Hazlett, Martin & Dom 1971) show that degenerating fibres reach the cerebellum via typical dorsal and ventral spinocerebellar tracts and that dorsal fibre tracts terminate ipsilaterally in the anterior lobe vermis and in the pyramis and paraflocculus of the posterior lobe. Ventral tract fibres project to the anterior lobe contralateral to the side of hemisection. In the anterior lobe, the distribution of degenerating fibres is in five saggital rows, symmetrically positioned around the midline. Three rows occur in the posterior lobe. In eutherians, seven to eleven rows are present suggesting that the relatively small number of rows in marsupials is a characteristic difference, perhaps with phylogenetic implications (Hazlett *et al*. 1971; Watson *et al*. 1976). Three main spinocerebellar pathways, the bulbothalamic mechanosensory and spinothalamic systems, have been identified in marsupials and their structure and organisation appears similar to those of eutherians.

The cerebellum in marsupials differs little in structure from that of eutherian species. Evidence suggests that the inferior olivary nuclear complex in metatherians has two nuclei directly homologous with eutherians, the dorsal and principal nuclei. The medial nucleus of eutherians (also known as the ventral or medial accessory olivary nucleus) is not found in marsupials, but may be homologous with a nucleus which lies lateral rather than medial to the other olivary nuclei (Watson & Herron 1977). Watson & Herron (1974) suggested that this difference, while minor, may reflect variations in the migration times of embryonic cells which form the olivary nuclei. Observations on the input ratio of inferior olivary cells to Purkinje cells in Brushtail Possums indicated that each inferior olivary cell sends climbing fibres to about fifteen different Purkinje cells (Furber & Watson 1979). Purkinje cells lie in the cerebellar cortex and function as the output channel for all cortical processing in the cerebellum.

The shape of the cerebellum varies greatly between marsupial species (Fig. 17.12b), depending on body size and also probably the complexity of muscular organisation and coordination (Johnson 1977). Parallel series of species with increasing cerebellar complexity can be seen both in the Eutheria and Metatheria (Johnson 1977). The basic organisation of the cerebellum in Metatheria is, however, quite constant. Intraspecific constancy is well demonstrated in Brushtail Possums which shows considerable phenotypic variation in the neocortices between individuals, yet little variation in the cerebellum (Haight & Neylon 1978a). A simple cerebellar cortex is seen in small insectivorous South American caenolestid and dasyurid marsupials, but the simplest mammalian cerebellar cortex is found in the Marsupial Mole (Burkitt 1938).

As in other vertebrates, the metatherian cerebellum functions primarily to control posture, using visual and vestibular inputs, and to coordinate skeletal muscle activity by using information from muscle proprioreceptors.

The basal ganglia of the telencephalon show no major structural or projection differences in marsupials when compared with those of eutherians. The globus pallidus is generally smaller in marsupials, but like the corpus striatum, which contains the caudate nucleus and putamen, it shows a typical mammalian organisation. The metatherian claustrum varies in size between species. In some macropodids, it is a very prominent component of the basal ganglia, but in didelphids it is difficult to find. The basolateral amygdaloid nuclei are well

defined in marsupials and the massa intercalatus, which extends between these nuclei, almost encloses the central nucleus to form a continuous wall (Johnson 1977).

The development of the neocortex and dorsal thalamus is a distinctive feature of the mammalian brain and marsupials, like eutherians, show a range of cortical development. Simple forms are found in caenolestids (Obenchain 1925) and the Marsupial Mole (Burkitt 1938) and the most complex cortical development occurs in some of the larger species such as kangaroos and wombats (Johnson 1977). The extreme cortical predominance found in some eutherians such as primates and cetaceans, however, has never been achieved in metatherians. The degree of convolution of the neocortex is related to body size and in marsupials is greatest in kangaroos and wombats, with the larger marsupiocarnivores showing a degree of convolution appropriate for their size.

Since differences in neocortical development and in associated structures between species contributes significantly to differences in brain weight, this has been used in various combinations to demonstrate grades of evolution in the various families of the Metatheria (Harman 1947; Filimonov 1949; Dillon 1963b; Elias & Schwartz 1969; Moeller 1973; Nelson & Stephan 1982). Using brain/ body weight ratios as an index of encephalisation, Mueller (1973) suggested that the Didelphidae and Macropodidae represented the lowest and highest grades of evolutionary development, respectively, in the four families examined. The Dasyuridae and Phalangeridae fell between these extremes. More recently, Nelson & Stephan (1982) made a more extensive analysis of brain/body weight relationships and developed a comparative index of encephalisation for Australian marsupials which incorporated an allometric analysis to account for body weight differences. These studies show that dasyurids, peramelids and burramyids have lower indices than phalangerids, macropodids and vombatids. They also demonstrate some anomalies within the Petauridae, which has indices amongst the lowest and highest for marsupials. Based on comparisons of marsupial and eutherian indices they concluded that, with respect to 'grade of evolution', marsupials lie between basal eutherian insectivores and lower prosimians.

Regionalisation of the metatherian cortex is generally indistinguishable from eutherians. The somatic sensory-motor neocortex is subdivided into specialised regions of function, like the Eutheria (Abbie 1940; Lende 1963a, 1963b, 1963c; Rees & Hore 1970). Similar somatic sensory projection to the neocortex has also been studied in various marsupials (Adey & Kerr 1954; Haight & Weller 1973; Johnson, Haight & Megirian 1973; Lende 1963a, 1963c; Magalhães-Castro, Saraiva & Magalhães-Castro 1971) and are known mostly to overlap related motor areas in the cortex: the sensorimotor amalgam (Lende 1963b, 1963c). This is in direct contrast to the situation in eutherians where sensory and motor regions of the cortex either are separated completely or show minor partial overlap. In *Didelphis*, input projection from the cerebellum and basal ganglia to the ventral thalamus is relayed to the same cortical regions as sensory information from the ventrobasal thalamus (Johnson 1977). In Brushtail Possums, however, cerebellar (motor) input to the anterior thalamus projects anteriorly in the sensory-motor cortex whereas somatic sensory projection to the ventrobasal thalamus is directed posteriorly (Johnson 1977). Motor and somatic sensory cortical regions in Brushtail Possums are not congruent and parts of the thalamus show an organisational complexity which contrasts with that of *Didelphis*, but resembles eutherians. Examples of the latter include the cytoarchitectural complexity of the postero-lateral nuclear complex, the ventral tier nucleus and the laminated lateral geniculate nucleus (Haight & Neylon 1978b, 1978c). In other thalamic features, such as the complexity and prominence of midline nuclei and the absence of a midline central nucleus, the thalamic configuration of Brushtail Possums resembles that of *Didelphis*.

Despite these differences and variations, however, metatherian thalamic organisation and projections to the neocortex more closely resemble the eutherian condition than that found in prototherian mammals (Lende 1969).

An important distinction in central nervous system organisation between eutherians and metatherians is the nature of their interhemispheric connections (Owen 1837; Abbie 1939b). Marsupials are acallosal (Fig. 17.12a), unlike eutherians in which the corpus callosum forms the most prominent and direct interconnecting commissure between the cerebral hemispheres. Marsupials generally rely on the same basic pattern of interhemispheric commissures found in prototherians (Abbie 1939b). These include the hippocampal and anterior commissures, the latter providing communication, via the external capsule, between the olfactory bulbs, basal ganglia, cerebral cortex and the amygdalar regions (Fig. 17.12a). An additional bundle of commissural fibres, the fasciculus abberans, which provides a more direct connection between the dorsal neocortex of each hemisphere, is found in all diprotodont marsupials. Fasciculus abberans fibres travel in the internal capsule and join the anterior commissure after passing through the corpus striatum (Smith 1902b; Abbie 1937). The fasciculus abberans has apparent phylogenetic implications since it clearly distinguishes diprotodont from polyprotodont marsupials (Abbie 1937).

Commissures associated with diencephalic structures also interconnect the cerebral hemispheres, for example the thalamic commissural fibres, the suprachiasmatic commissure, the posterior commissure, the habenula commissure and the optic chiasma (Johnson 1977).

The autonomic and peripheral nervous system in marsupials have largely been ignored. The sparse information available (Barbour 1963; Kiozumi & Sato 1964; Voris 1928a, 1928b) does not suggest any major differences in structure or function between marsupials and eutherians with respect to these systems. In *Didelphis*, Kiozumi & Sato (1969) suggested a difference in autonomic regulation of blood pressure based on a prominent sympathetic innervation of carotid baroreceptors. The peripheral lumbar and brachial plexuses of Brushtail Possums show close structural similarities to those of eutherians (Barbour 1963).

Central nervous system structures showing convergent evolution can be found in the metatherian brain. The multilaminated lateral geniculate nucleus in phalangerid marsupials is an excellent example of convergence with a similar structure in primates (Hayhow 1967), as is the occurrence of barrels in the neocortex of rodents and phalangerids (Weller & Haight 1973). Both these examples may prove useful for examining factors such as arboreality and vision, which affect selective mechanisms in the evolution of the central nervous system (Johnson 1977).

Developmental studies of the metatherian nervous system are few and mostly confined to *Didelphis* (McCrady *et al*. 1937; Larsell *et al*. 1944; Morest 1968, 1970). The only detailed studies of an Australian species have been in the Tammar Wallaby (Renfree *et al*. 1982a; Reynolds *et al*. 1985) (Fig. 17.13). A rapid growth phase of the brain occurs in the first 180 days of pouch life, during which brain weight increases from 9 mg–12 g (60% of adult brain weight). A slower linear growth phase then ensues with 85% of adult brain weight reached after 480 days. The transition from rapid to mature growth phases for each brain component occurs between 120 and 180 days postnatally. This coincides with transitions in other body functions, for example the acquisition of thermoregulation, thyroid function, metabolic rates of various organ systems and Na^+/K^+ ratios in brain tissue.
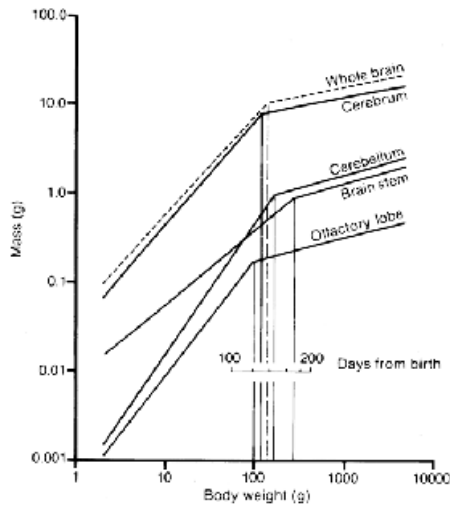
Figure 17.13 Allometric relationships between the growth of the whole brain and some of its components in the Tammar Wallaby from early pouch life to maturity. Log brain weight (mass) plotted against log body weight show rapid and mature growth phases in whole brain and its components with some variations in allometric rates of components during the rapid growth phase (for example compare the growth rate of brain stem with cerebellum). The transition between these two growth phases when body weight is between 95 and 259 g (*i.e.* between 124 and 172 days of pouch life). (Redrawn from Renfree *et al.* 1982a)

ENDOCRINE SYSTEMS

(i) Reproductive endocrine systems.

Most of the reproductive endocrine glands of Metatheria and their function are discussed in the section on reproduction below.

Hypothalamus. The metatherian hypothalamus appears similar in its structure and relationships to that of eutherians (Johnson 1977), although detailed anatomical descriptions are restricted to a few studies on *Didelphis* (Bodian 1939; Wislocki 1940; Oswaldo-Cruz & Rocha-Miranda 1967) and the macropodid, the Tasmanian Pademelon, *Thylogale billardierii* (Johnson 1977). Cell bodies in the supraoptic and paraventricular nuclei of the hypothalamus of *Didelphis* send axons through the infundibulum to the neurohypophysis (Bodian 1939; Wang 1969) which transport various hormones, such as antidiuretics (arginine vasopressin) and oxytocin (Ferguson & Heller 1965), for release from the neurohypophysis. Releasing hormones, such as gonadotrophin-releasing hormone (GnRH), are also probably secreted from the marsupial hypothalamus, but no attempt has yet been made to extract or characterise them. In eutherians these are synthesised and secreted by the hypothalamus and act on the adenohypophysis to release various pituitary-derived protein hormones.

The involvement of the hypothalamus in thermoregulation and in sexual and other specific behavioural patterns has been demonstrated in *Didelphis* (Roberts *et al*. 1967). Supraoptic lesion in the hypothalamus of the Tammar Wallaby has been shown to induce diabetes insipidus (Bakker & Waring 1976).

Pituitary. Like the hypothalamus, there is little structural information on the marsupial pituitary. The more comprehensive studies of metatherian pituitary function (Hearn 1974, 1977; Gallo *et al*. 1978; Evans, Tyndale-Biscoe & Sutherland 1980; Tyndale-Biscoe & Evans 1980) do demonstrate, however, that close similarities to the eutherian pituitary exist, suggesting a general similarity in structure. The pituitary is located in the ventral midline of the brain (Fig. 17.12a) inside the sphenoid- derived sella turcica. It typically comprises the neurohypophysis (posterior lobe) and adenohypophysis (anterior lobe) (Ortman & Griesbach 1959; Leatherland & Renfree 1983b). Little specific structural information is available on the neurohypophysis (Johnson 1977). Studies have been made on the structure of the pars distalis in two macropodids (Ortman & Griesbach 1959; Leatherland & Renfree 1983b). Somatotrophic,

mammotrophic, corticotrophic, luteotrophic, thyrotrophic and folliculotrophic cells and their distributions are known in three regions of the pars distalis of the Tammar Wallaby (Leatherland & Renfree 1983b).

Pharmacologically active principals from the metatherian neurohypophysis, such as oxytocin, vasopressin and phenypressin, have been isolated and characterised in five macropodids, the Common Brushtail Possum and three didelphids (see Tyndale-Biscoe & Renfree 1987; Chapter 29 this volume).

Pineal. Pineal morphology has been examined in a few metatherians: the Virginia Opossum (Jordan 1911), the Red Kangaroo, the Eastern Grey Kangaroo (Quay 1966) and the Long-nosed Potoroo, *Potorous tridactylus* (Bradley 1972). The pineal and habenulae form the epithalamic complex, situated between the third ventricle of the brain and extracerebral fluid above the thalamus (Johnson 1977). In marsupials, the pineal varies in shape and position between and, sometimes, within species (Jordan 1911; Machado 1965; Johnson 1977). In macropodids, the pineal has an extensive vascular supply with coiled anastomosing chains of capillaries and sinusoids extending between the pineal lobules (Quay 1966).

The pineal is responsive to photoperiodic stimuli (McConnell & Tyndale-Biscoe 1985; McConnell 1986; McConnell, Tyndale-Biscoe & Hinds 1986) and release of melatonin can be prevented directly by pinealectomy or indirectly by transection of the sympathetic innervation of the pineal (Renfree *et al*. 1981a; Renfree & Short 1984; McConnell & Hinds 1985). The enzyme associated with melatonin secretion, hydroxy-indole-o- methyl-transferase (HIOMT), has been identified in two macropodids (Bradley 1972; Kennaway & Seamark 1975). A significant fall in HIOMT activity in the Tammar Wallaby pineal occurs at the time of the summer solstice (Kennaway & Seamark 1975). The effects of reduced HIOMT levels on melatonin secretion in this species is not known.

In the Tammar Wallaby and the Red-necked Wallaby, *Macropus rufogriseus*, melatonin treatment causes termination of embryonic diapause (Renfree & Short 1984; Loudon, Curlewis & English 1985; McConnell & Tyndale-Biscoe 1985), probably by indirect action on pituitary function via the hypothalamus.

(ii) Adrenal

Adrenal gland structure and location have been examined in detail by Bourne (1949) and Jones (1957). Adrenocortical functions have been extensively studied (McDonald 1977; McDonald & Waring 1979; Weiss 1984).

The marsupial adrenal is very similar in structure to the eutherian gland, consisting of a central medulla, which may reach the adrenal surface in some species and a peripherally arranged cortex with clearly defined cortical zones (Bourne 1949; Bolliger 1953; Jones 1957; McDonald 1977). The only known major deviation from this pattern occurs in Common Brushtail Possum females, where an additional eccentrically placed zone of hypertrophied cortical tissue, known as the special zone, is located between the zona fasciculata and zona reticularis. This zone is absent in female pouch young and ill-defined in young virgin females, but is conspicuous in adult females during oestrus, pregnancy and lactation (Bourne 1949). At these times, it contributes from 19%–55% of adrenal gland volume (Call & Janssens 1984). The steroidogenic function of this zone appears to differ from the cortex proper since Weiss & Ford (1982) have identified, in addition to the usual hydroxylation enzymes, active 5α and 5ß reductases and C_{17-20}lyase. Special zone development and steroidogenic function can be induced in immature female pouch young by treatment with FSH (follicle-stimulating hormone) (Weiss 1984). FSH and oestradiol induce changes in the pattern of steroidogenesis in the special zone of mature females. Risbridger & Weiss (1985) have shown FSH, but not LH/HCG or progesterone,

binding activity in both the special zone and cortex proper and a specific binding affinity for oestradiol by cells in the cortex proper. The physiological significance of these observations, however, remains unexplained.

Cortisol is the major glucocorticoid in adrenal and peripheral venous blood of marsupials (McDonald & Waring 1979) although in a few species, corticosterone or 11-deoxy-cortisol is found in equal or higher concentrations (Oddie *et al*. 1976; McDonald & Bradshaw 1977). In each of these species, adrenocorticotrophic hormone (ACTH) stimulates significant rises in peripheral venous concentrations of cortisol. Aldosterone and deoxycorticosterone have been identified in various species (Oddie *et al*. 1976; McDonald 1977) and 21-deoxycortisol has been identified in moderate to high concentrations in all metatherians examined (McDonald & Waring 1979).

As in eutherian mammals, corticosteroid secretion in marsupials is controlled directly by ACTH secretion from the pituitary. This can be modified by stress, various other environmental influences and by treatment with pharmacological agents such as dexamethasone (Vinson, Tyndale-Biscoe & Bancroft 1973). Hypophysectomy (Hearn 1977) and unilateral adrenalectomy (Reid & McDonald 1968b) are known to affect intact adrenal size. Hypophysectomy caused a rapid decline in peripheral concentration of corticosteroid and adrenal gland hypotrophy. Unilateral adrenalectomy results in cortical hypertrophy of the remaining adrenal.

In general, marsupials have a low sensitivity to eutherian or synthetic ACTH (McDonald 1977; McDonald & Waring 1979). Infusion of porcine ACTH in Tammar Wallabies, however, caused an immediate and sustained elevation of plasma corticosteroid levels and a subsequent rise in blood glucose concentration (Cooley & Janssens 1977). ACTH also appears to have a direct action on the adrenal medulla, releasing adrenaline which in turn increases the concentration and turnover of blood glucose (Janssens & Tyndale-Biscoe 1982).

The metabolic effects of corticosteroids in marsupials are reviewed by McDonald (1977) and McDonald & Waring (1979). The strongly immunosuppressive effects of a rise in free glucocorticoid levels in males of the Brown Antechinus, *Antechinus stuartii*, during the breeding season appears to be an indirect cause of seasonal male die-off, which characterises this and other small dasyurids (Bradley 1977). In most species (Khin Aye Than & McDonald 1974; Cooley & Janssens 1977; McDonald & Waring 1979), infusion of glucocorticoids causes a typical eutherian response on carbohydrate (hyperglycaemia) and nitrogen metabolism (nitrogen mobilisation). In contrast, however, the Red Kangaroo and the Quokka, *Setonix brachyurus*, are insensitive to the diabetogenic and nitrogen-mobilising effects of glucocorticoids (Griffiths, McIntosh & Leckie 1969b; McDonald & Waring 1979), even in extremely high doses, although a transient nitrogen-mobilising effect can be evoked in male *Setonix*. Glucocorticoid insensitivity in these species may have evolved as an adaptation to habitats in which dietary nitrogen is a seasonally limiting resource (McDonald 1977).

Several experimental studies suggest that some marsupials may be less dependent on their adrenals than eutherians. The Virginia Opossum, like the monotreme Echidna, *Tachyglossus aculeatus* (McDonald & Augee 1968), can normally survive without saline or steroid supplements after bilateral adrenalectomy, providing it is not subjected to stress (Hartmann *et al*. 1943). The Red Kangaroo also is unaffected, providing it has access to saline to maintain normal plasma Na^+ concentrations (McDonald 1977). In contrast, the Quokka has a mean survival time of 36 hours following bilateral adrenalectomy. With saline, whole cortical extracts or glucocorticoid treatment this could only be extended to 5 days.

Pancreas

The pancreas of marsupials comprises exocrine and endocrine components which are similar to those of other mammalian groups (Griffiths 1965a; Munger, Caramia & Lacy 1965; White & Harrop 1975; King, Krause & Cutts 1978). It is usually located in the mesoduodenum, where it drains into the duodenum via the pancreatic duct. In most species the pancreas is diffuse, but in the Koala and the Common Wombat it is more compact (Mackenzie 1918b; Osgood 1921; Sonntag 1921a; Jones 1948). Considerably more is known about the endocrine structure and function of the marsupial pancreas than its exocrine components (King *et al*. 1978).

Four endocrine cell types have been identified in the pancreatic islets of the Virginia Opossum (Munger *et al*. 1965); three are similar to those seen in eutherians and one appears to be unique (Thomas 1937).

As in eutherians, insulin causes a rapid hypoglycaemia in marsupials which can be antagonised by glucocorticoids in Brushtail Possums, but not in the two macropodids studied (McDonald 1977). In Brushtail Possums, insulin causes an unexpected increase in plasma free fatty acid concentration, but a normal reduction in plasma amino nitrogen.

Alloxan treatment in marsupials causes a typical eutherian-like degeneration of the islets and induction of diabetes mellitus which can be controlled by insulin treatment (Adams & Bolliger 1954; Barker 1961; Griffiths *et al*. 1969b).

Thyroid and parathyroid

From the few observations which have been made, thyroid structure and function in marsupials appears to be similar to that of eutherians (Barbour 1977; McDonald & Waring 1979). The thyroid has two lobes which are situated in the neck on either side of the thyroid cartilage and trachea and sometimes connected ventrally by a narrow isthmus of thyroid tissue (Fraser 1915; Sonntag 1921a; Kingsbury 1940; Adams 1955).

The little comparative information available on the histology or ultrastructure of the metatherian thyroid was provided by Azzali (1964) and Fortney (1978). Krause & Cutts (1983a) described changes in thyroid structure of *Didelphis* from birth. In the Tammar Wallaby, the thyroid has been examined during three stages of development (Setchell 1974a, 1974b). At about 180 days after birth, follicular diameter and epithelial height is indistinguishable from adult thyroids. A period of rapid increase in these parameters occurs between days 140 and 180, coinciding with the transition from ecto- to endothermy (see Macropodidae Chapter 29).

Thyroid hormone-binding proteins have been identified in several marsupials (Davis, Gregerman & Poole 1969; Davis & Jurgelski 1973) and generally both thyroxine (T_4) and tri-iodothyronine (T_3) compete for binding sites on these proteins. In the Virginia Opossum these proteins are postalbumins, related to haptoglobins, whereas in the Red Kangaroo, the major binding protein is a prealbumin (Davis & Jurgelski 1973). Despite lower metabolic rates, marsupials have similar free plasma thyroxine levels to eutherians under normal basal conditions and similar basal rates of thyroid hormone secretion (Setchell 1974a, 1974b).

Total thyroid hormone levels in plasma of marsupials are generally considerably lower than in eutherians. The lower binding affinity of metatherian binding proteins for thyroid hormones in plasma, however, results in free plasma T_4 and T_3 levels similar to or greater than eutherian levels. Free T_4 concentration in plasma is similar in the Long-nosed Potoroo and the Tammar Wallaby (Setchell 1974a; Nichol 1977). Low environmental temperature causes an increase in

plasma T_4 levels under field conditions in the Tammar Wallaby (Kaethner & Good 1975), though no appreciable change under controlled laboratory conditions (Setchell & Good 1973). Thyroid stimulating hormone (TSH) levels in plasma are elevated throughout the period of cold exposure, causing a concomitant increase in T_4 release from the thyroid, suggesting an increased turnover of T_4 under the laboratory conditions.

Thyroidectomy causes a significant fall in metabolic rate in peramelids (Hulbert & Augee 1982b). Ablation of the corpus luteum in the Tammar Wallaby results in a significant decline in plasma total and free thyroxine (Leatherland & Renfree 1982). Only T_3 levels in plasma are increased by subsequent progesterone treatment.

Marsupials are usually endowed with two pairs of parathyroid glands, neither of which is associated directly with the thyroid. The general structure and distribution of parathyroids has been described in various marsupials (Fraser 1915; Adams 1955; Krause & Cutts 1983b): parathyroid III is usually found at or close to the carotid bifurcation whereas parathyroid IV is usually intrathoracic and often adjacent to the thymus. In the Virginia Opossum the parathyroids contain a single cell type, the chief or principal cell. Ultrastructural studies confirmed a protein synthetic capacity with a basally-directed release of secretory products into the extracellular space (Krause & Cutts 1983b). The function of the metatherian parathyroids has not been examined, but is probably similar to that of eutherian mammals.

Other endocrine systems

Little is known about endocrine cells and/or tissues in the gastrointestinal and urinary systems of marsupials. Some detailed studies, however, have been made on the renin-angiotensin system which acts to regulate blood pressure by peripheral vasoconstriction, to control the rate of aldosterone secretion and perhaps help to regulate intrarenal blood flow and filtration (Blair-West & Gibson 1977). Johnstone, Davis & Hartcroft (1967) and Blair-West et al. (1968) identified renin activity in kidney extracts of American and Australian marsupials. Juxtaglomerular complexes have been identified in a few marsupials (Blair-West et al. 1968; Reid & McDonald 1968b, 1969). Although typical renin granulation is not known, the importance of the kidney in the synthesis and secretion of renin is clearly demonstrable experimentally (Blair-West et al. 1967). In two marsupial species, sodium- depletion results in structural changes in the juxtaglomerular complexes which are consistent with renin storage (Johnstone et al. 1967; Reid & McDonald 1969).

The regulation and function of the metatherian renin-angiotensin system has not been studied. Little is known about the physiological effects of angiotensin II in marsupials except in Brushtail Possums, where infusion of angiotensin causes elevated peripheral levels of plasma aldosterone (McDonald & Waring 1979).

EXOCRINE SYSTEMS

Three pairs of salivary glands, similar in structure to those of eutherians, are usually present in marsupials (Osgood 1921; Forbes & Tribe 1969; Barbour 1977). Parotid glands are well developed in many diprotodont marsupials, in particular the Macropodidae, but are smaller in most polyprotodonts (Forbes & Tribe 1969). They appear to be absent in the Koala (Forbes 1881). Sublingual glands are variable in size throughout the Metatheria. The submandibular glands are generally larger in polyprotodonts than in diprotodonts (Barbour 1977). Histological studies on salivary glands in marsupials (Forbes & Tribe 1969; Quintarelli & Dellovo 1969; Wilborn & Shackleford 1969) showed the parotid

and sublingual glands to comprise serous and mucous secreting cells, respectively, and the submandibular gland to be a mixed gland containing mostly serous but also mucus secreting elements. Biochemical studies on saliva are limited to the Macropodidae, in which high concentrations of Na^+ and HCO_3 ions and amylase activity have been recorded. Beal (1984) described in detail the electrolyte composition of saliva from sodium-replete Red Kangaroos. Some species of Petauridae use salivary odours for social communication (Schultz-Westrum 1965).

Marsupials are well endowed with cutaneous glands which have various functions, as in other vertebrates. Holocrine sebaceous glands and apocrine sudoriferous glands are common and widely distributed over the body (Hardy 1947; Green 1963a; Mykytowycz & Nay 1964; Kean 1966).

In the skin of most Metatheria, hairs are organised in groups consisting of a larger central hair, associated with a large sebaceous gland and apocrine gland, and lateral hair clusters each with their own sebaceous gland (Green 1963a; Mykytowycz & Nay 1964). Sebaceous glands occur in all parts of the body covered with hairy skin except at or near mucocutaneous junctions such as the edges of the lips, anal region, nipple and glans penis (Green 1963a), where they lie unassociated with hairs. In the four species examined by Green (1963a), sebaceous glands are morphologically similar; the only apparent structural variations are in the numbers of alveoli which constitute the gland mass. Each alveolus consists of an outer layer of basal cells and an inner core of secretory cells which vary considerably in size and are sometimes replaced by a central lumen. Each alveolus is connected by a short duct to the main secretory duct which is characterised by a stratified squamous epithelium and which becomes continuous with the outer root sheath of the hair.

Apocrine gland structure is also uniform in the species so far examined. As in eutherians, metatherian apocrine glands are coiled tubules located deep within the dermal layer at or near the base of the hair follicles. Those differences observed between and within species simply reflect different phases of secretory activity, rather than a structural difference in the usual coiled structure of the gland (Green 1963a).

Eccrine sweat glands have been found only in association with non-hairy ventral skin of the paws and, in some species (for example, the Common Brushtail Possum), the tail (Bentley 1955; Green 1961; Mykytowycz & Nay 1964; Fortney 1973). In all species examined, these glands consist of loosely coiled secretory tubules surrounded by a connective tissue capsule. The shape and size of sweat glands vary with body size, age and sex (Mykytowycz & Nay 1964). In macropodids the largest and most complex glands are found in males in skin over the sternum, axilla and scrotum. The function of sweat glands in the thermoregulation of marsupials has been discussed by various workers (Green 1961; Dawson 1983).

Scent-producing glands are common in the Metatheria and have been described so far in some 63 species in 40 of 73 extant genera (Russell 1985).

Although the importance of olfaction in metatherian communication has been the subject of few studies (Schultz-Westrum 1965; Eisenberg & Golani 1977; Biggins 1984) the structure, distribution and function of scent-producing glands in marsupials have received considerably more attention and are thoroughly reviewed by Russell (1985).

Paracloacal glands, also known as anal or paraproctal glands, are the most widely distributed scent glands in Metatheria. They occur in all species which have been examined and appear as small cystic structures which lie in pairs along the lateral walls on either side of the cloaca. Between one and four pairs occur, depending upon species, and each drains by a narrow duct into the cloaca.

Each gland is invested in a thin, striated muscle capsule containing penetrating apocrine glands which either open into the cloacal gland ducts or directly into the cloaca. The secretory cells are arranged in several layers along radially projecting connective tissue septa which penetrate into the lumen from a thin layer of connective tissue lining the inner surface of the muscular capsule.

Two different types of paracloacal glands have been identified: oil-secreting glands, producing a pale yellow, pungent secretion containing emulsified oil droplets in an aqueous phase, and; cell-secreting glands, which secrete an odourless cell suspension in aqueous phase (Bolliger & Whitten 1948; Green 1963a). The oily secretion is often released during handling in some marsupial species. It is also often a component in urine, coated on faeces and used during specific marking behaviour. The cell secretion is either voided in the urine or associated with faeces.

Both oil and cell-secreting glands are found in some species (Bolliger & Whitten 1948; Thomson & Pears 1962; Green 1963a), but in many species only one gland type occurs. Examples of the latter include the Long-nosed Bandicoot (Bolliger & Whitten 1948) and probably most macropodids (Russell 1985) where only cell-secreting paracloacal glands are found, and the Common Ringtail Possum (Bolliger & Whitten 1948), the Southern Brown Bandicoot (Green 1963a) and various species of Petauridae (Schultz-Westrum 1965; Smith 1984a) in which only oil-secreting glands are present. Lipid components of paracloacal gland secretions have been examined in the Sugar Glider, *Petaurus breviceps,* (Autrum, Fillies & Wagner 1970) and the Common Brushtail Possum (Biggins 1979). Differences in paracloacal gland size appears to be linked to reproductive status in the Sugar Glider (Smith 1984a), but not in the Western Pygmy-possum, *Cercartetus concinnus* (Smith 1984b).

Sternal glands are also widespread and important odour-producing glands in marsupials, although they have not been identified in all species (Green 1963a; Thompson & Owen 1964). In general, sternal glands are larger in adult males and many species show seasonal variations in gland size and secretory activity. A bare patch of skin indicates the location of the sternal gland in species like the Numbat (Ford 1934) or the Sugar Glider (Schultz-Westrum 1965). Often, however, its location is indicated, especially in mature males, by a brownish-red coloration of the hair covering the glandular patch, caused by internal and external pigmentation of the hair shaft (Nicholls & Rienits 1971).

Marsupial sternal glands are rather uniform in structure, comprising sebaceous and apocrine sudoriferous glands which are both usually, though not always (see Macropodidae Chapter 29), larger and more active than sebaceous and apocrine glands in adjacent areas of skin. Often, especially in reproductively mature animals, hair over the sternal gland is moist with secretion which has a distinct odour (Bolliger & Hardy 1944; Mykytowycz & Nay 1964) and differs from paracloacal secretions in having higher concentrations of volatile components (Biggins 1979, 1984). Sternal glands are used in association with marking behaviour (Russell 1985).

Other types of odour-producing glands have been identified in various marsupial species. Pouch glands, containing varying ratios of apocrine and sebaceous elements, are common in female marsupials (Mykytowycz & Nay 1964; Schultz-Westrum 1965) and are usually more developed than sternal glands. These glands appear to produce a pigment in sexually mature females which stains pouch associated hairs reddish-brown. Secretions from pouch glands may assist neonates in locating the pouch after birth, in providing identifying odours for individual pouch young and for humidifying the marsupium.

Extensive auricular glands occur in some dasyurids and peramelids (Jones 1948; Green 1963a; Stoddart 1980), usually associated with the external auditory meatus and opening into it or onto an adjacent area of skin, often by a common

duct. These glands are usually characterised as sebaceous masses which may or may not be associated with enlarged tubular apocrine glands. In male bandicoots, the activity of these glands increases during the breeding season. Copious quantities of a pungent secretion are produced (Stoddart 1980).

Frontal glands, comprising holocrine, apocrine and sebaceous glands, occur in males of the genus *Petaurus* (Schultz-Westrum 1965) and produce an oily fluid with a musky odour which is used in social communication. Sebaceous chin glands which are prominent in males, have been reported in the Common Brushtail Possum (Winter 1975), In some species, a prominent glandular region has been observed around the oral cavity, especially at the mucocutaneous junction of the lips (Green 1963a). Behavioural evidence indicates that odours from the oral region are an important component of social communication in marsupials.

Other cutaneous exocrine glands. Various other cutaneously-derived and located exocrine glands have been identified in marsupials. Mammary glands are described below. Nasal vestibular glands, various sebaceous (Meibomian and Zeis) and serous type glands (Harderian) associated with the ocular region have been described in a few marsupials and lachrymal gland tissue has been identified in Brushtail Possums (Green 1963a).

REPRODUCTION

Genetics

The diploid chromosome complement of the Metatheria varies between 10 and 32, with 2N = 14 and 2N = 22 as the most common classes (Sharman 1961a; Hayman 1977; see also Chapter 19). G-banding studies have shown that the karyotype is so highly conserved that the same 2N = 14 banding pattern is retained in many Australian and American marsupial lineages. This pattern is presumed to be ancestral for all extant marsupials (Rofe & Hayman 1985). Most of the other karyotypes seen in marsupials can be derived from the ancestral karyotype by fissions, fusions and simple rearrangements (Chapter 19; Rofe 1979). Supernumerary chromosomes also have been described in marsupials (for example, the Greater Glider, *Petauroides volans*, McKay 1984).

The sex determining mechanism in marsupials is based on an XX (female) and XY (male) system, as in eutherians. The basic Y chromosome, however, is normally much smaller in marsupials than in eutherians. There are also many examples of independently derived X chromosome / autosome and Y chromosome / autosome fusions in marsupials (Sharman 1961a; Hayman 1977). No synaptonemal complex is formed between the X and Y chromosomes during male meiosis in the 22 marsupial species examined and, therefore, no possibility of exchange between these chromosomes in these species (Sharp 1982). Several loci are found on the X chromosome of both eutherians and marsupials (for example, glucose-6-phosphate dehydrogenase, Richardson, Czuppon & Sharman 1971; phosphoglycerokinase, Cooper *et al*. 1971) and it seems likely that the X chromosome has been conserved intact in these taxa since their common origin over 100 mybp. Dosage compensation of X chromosome linked loci in somatic tissues is achieved by inactivation of one X chromosome in each female cell, leading to a single active X in both male and female cells. Unlike the situation in eutherians, however, where inactivation is unrelated to the origin of the X chromosome (that is, random X inactivation), it is the paternally derived X chromosome that is inactivated in the somatic tissues of marsupials (Richardson *et al*. 1971; Cooper *et al*. 1971; Sharman 1971). In several

marsupial lineages (including unrelated peramelid and phalangerid species), the inactivated X chromosome is eliminated in some somatic cell lines, leading to an apparent XO condition (McKay 1984; Clare 1984).

Female Reproductive Tract

Gross anatomy. Female marsupials have two ovaries, two oviducts and two uteri, like other mammals, as well as a unique vaginal apparatus that opens into a urogenital sinus, which also receives the urethra (Tyndale-Biscoe & Renfree 1987). The urogenital sinus, together with the hind gut, opens caudally into the urogenital opening. The double but completely separate uteri, characteristic of all marsupials, open by separate cervices: unlike many species of Eutheria, no marsupial has a single chambered uterus.

The oviduct has not been well studied, possibly because the eggs pass through it so rapidly, but has recently been described with ultrastructural techniques (Armati-Gulson & Lowe 1985; Arnold & Shorey 1985). The musculature consists of inner circular and outer longitudinal layers which allow peristaltic movement. The mucosal lining consists of a folded, simple ciliated columnar epithelium interspersed with mucus secreting cells (Andersen 1928). In most marsupials, the oviduct is long and convoluted so the transport of the eggs must involve muscular contractions (Hartman 1924). The oviducts vary considerably between species in length and in the degree of convolution.

The paired, but separate, uteri consist of an inner, glandular endometrium and an outer, muscular myometrium. In monovular species the uteri are well-defined fusiform bodies, with their posterior extremities lying close together on each side of the median line and loosely joined by connective tissue (Pearson 1944a) and the round ligament (Tyndale-Biscoe 1968). The parallel uterine necks open into the vaginal culs-de-sac by two separate cervices which may be up to 10 mm or so in length. The myometrium consists of an outer longitudinal and inner circular layer of muscle, with some oblique muscle fibres (Lierse 1965).

The vaginal canals are the most variable part of the anatomy of the female tract and much of the early work concentrated on their gross anatomy (Tyndale-Biscoe & Renfree 1987). These were reviewed first by Lister & Fletcher (1881) and Fletcher (1881, 1883) and subsequently by Nelsen & Maxwell (1942), Pearson (1945), Eckstein & Zuckerman (1956) and Barbour (1977).

The vaginal apparatus consists of two lateral vaginae, each connecting the uterus of the same side to the urogenital sinus. The anterior end of each lateral vagina, separated only by a common median septum, unite into a vaginal cul-de-sac, into which the uterine cervices open (Tyndale-Biscoe & Renfree 1987). The more posterior regions of the lateral vaginae form the urogenital strand together with the ureters and urethra in a mass of connective tissue. Externally, the strand is composed of relatively thick fibrous connective tissue (Nelsen & Maxwell 1942). Posteriorly, the two canals may unite for a short distance before joining the urogenital sinus.

In most species of Macropodidae and in the Honey Possum, the birth canal (median vagina) remains open after the first parturition and becomes lined with the cuboidal epithelium of the culs-de-sac merging with the stratified squamous epithelium of the urogenital sinus (Tyndale-Biscoe & Renfree 1987). In the majority of marsupials, however, there is no permanent birth canal. A pseudovaginal canal forms in the connective tissue strand between the ureters prior to each parturition. The connective tissue cleft closes rapidly after passage of the young and the epithelia of the urogenital sinus and the vaginal culs-de-sac reunite so that no indication of the pseudovaginal canal remains (Tyndale-Biscoe 1966). This pattern of regular opening and closure of the passage associated with parturition occurs in the families Didelphidae, Caenolestidae,

Dasyuridae, Peramelidae, most species of Phalangeridae, all Potoroidae and in the Banded Hare-wallaby, *Lagostrophus fasciatus*, and the Eastern Grey Kangaroo, *Macropus giganteus*, among the Macropodidae.

The septum separating the right and left vaginal culs-de-sac may be present throughout life with the latter small, just covering the cervices which project through them, as in *Antechinus* and the opossum *Marmosa* (Hill & Fraser 1925; Pearson & de Bavay 1951, 1953). These marsupials, and others that give birth to the smallest young (Peramelidae, Dasyuridae and Didelphidae), have the smallest vaginal culs-de-sac, the most complete septa and the greatest distance between the cervices and the urogenital sinus (Tyndale-Biscoe & Renfree 1987). The exception is *Tarsipes*, which gives birth to the smallest mammalian young recorded, yet has a permanently open birth canal (de Bavay 1951; Renfree 1980a and unpublished data). The species which have the largest neonates have very large culs-de-sac, an incomplete (or absent) median septum and a short pseudovaginal canal which may remain permanently open after the first birth (Sharman 1965).

Histology

During the pro-oestrus phase, through oestrus and post-oestrus, the endometrial glands and epithelia undergo hyperplasia (Tyndale-Biscoe & Renfree 1987). In the monovular Common Brushtail Possum this lasts about 7 days (Shorey & Hughes 1973). In the polyovular *Didelphis*, there is no difference in total volume, endometrial width and glandular abundance at days three and seven of pregnancy or the oestrus cycle (Fleming & Harder 1981).

By the time the corpus luteum is formed in the Eastern Grey Kangaroo, the uterine glands are numerous but scattered, with small lumina frequently containing sperm (Clark & Poole 1967).

During the follicular phase, the vaginal complex and the urogenital sinus enlarge by hyperplasia and hypertrophy, reaching a maximum at oestrus when the total weight may be several times as great as in the quiescent or anoestrus state (Tyndale-Biscoe & Renfree 1987). The mucosal lining of cuboidal epithelium of the median vagina and vaginal caecum is highly secretory at oestrus (Risman 1947; Hughes & Rodger 1971). Conversely, the lateral vaginae and urogenital sinus are lined with the squamous epithelium (Barbour 1977) which becomes cornified and is sloughed in clumps into the lumina of the lateral vaginae (Clark & Poole 1967). The lateral vaginae are responsive to the presence of follicular oestrogens (Short, Flint & Renfree 1985). After copulation, the semen passes up the lateral vaginae to the median vagina where it mixes with the mucus and coagulates. Like the oviducts, the lateral vaginae are highly motile and undergo active peristalsis at oestrus (Hartman 1924) which may facilitate this transport and mixing.

The entire vaginal complex decreases in size post-oestrus, whilst the uteri become highly secretory, more vascular and oedematous (Von der Borch 1963; Renfree 1972b; Renfree & Tyndale-Biscoe 1973a). The cuboidal gland cells with large central nuclei become transformed to tall columnar cells with small, basally situated nuclei and chromophobic cytoplasm (Sharman 1955a; Clark & Poole 1967). At the end of the luteal phase, the glands of the endometrium and their epithelial cells regress and the sub-epithelial stroma shrinks.

In lactating macropodids or in seasonally breeding species, there may be a quiescent phase in which the uteri remain small but not flaccid as in anoestrus (Tyndale-Biscoe, Hearn & Renfree 1974; see Macropodidae Chapter 29). The uterine glands are numerous and irregularly scattered, with connective tissue between them and their cells are columnar with round basal nuclei (Clark & Poole 1967). No mitoses are observed and the lining of the uterine lumen has both ciliated and non-ciliated cells.

Folliculogenesis

The growth of the oocyte and its associated follicles have been examined by Lintern-Moore *et al*. (1976, 1977). Alcorn (1975) gives a detailed description and analysis of ovarian development during pouch life in the Tammar Wallaby. The development of follicles in prepubertal females and the role of the pituitary in this have been examined only in the Tammar Wallaby (Hearn 1972a, 1975a; Alcorn 1975; Panyaniti *et al*. 1985).

In Eutheria, antrum formation is dependent on pituitary gonadotrophin and this is probably true for marsupials (Tyndale-Biscoe & Renfree 1987). In the Tammar Wallaby, the increase in oocyte and follicular diameter is blocked after hypophysectomy (Hearn 1972a, 1975b). In species that undergo true anoestrus, such as the Virginia Opossum (Hartman 1923; Martinez-Esteve 1942), the Greater Glider (Smith 1969), the Quokka (Sharman 1955a) and the Common Brushtail Possum (Tyndale-Biscoe 1955), the ovaries become small and contain only small follicles 0.2 mm in diameter.

The number of follicles that ovulate varies widely in marsupials (Tyndale-Biscoe & Renfree 1987). In the Virginia Opossum, Hartman (1921) records a maximum of 56, with 20 abnormal. Similarly, in *Didelphis marsupialis* (= *aurita*) Hill (1918) recorded more than 20 eggs shed at one ovulation. Godfrey (1975) also recorded 12 to 27 follicles or corpora lutea in *Marmosa robinsoni*. The ovulation rate of the South American marsupials *Dromiciops* and *Caluromys*, however, is less than four. In all the Dasyuridae examined, the Eastern Quoll, *Dasyurus viverrinus* (Hill 1910), the Tasmanian Devil (Flynn 1922; Guiler 1970b; Hughes 1982a), the dunnart *Sminthopsis larapinta* (Godfrey 1969a), the Brown Antechinus (Woolley 1966a, 1966b) and in the Kowari, *Dasyuroides byrnei* (Woolley 1971), ovulation rates are high.

In the Peramelidae and Burramyidae, the ovulation rate is low and the number of corpora lutea generally equals the number of young in the pouch (Clark 1967; Lyne & Hollis 1979). The herbivorous monotocous species are almost invariably monovular and, on circumstantial evidence, it generally has been supposed that the ovaries ovulate alternately in successive cycles (Tyndale-Biscoe & Renfree 1987). After ablation of one ovary, however, female Tammar Wallabies ovulate in successive cycles from the remaining ovary.

Male Reproductive Tract

Gross anatomy. The male reproductive system of marsupials consists of paired scrotal testes and epididymides connected by vasa deferentia to the postero-lateral surface of the prostatic urethra close to the bladder neck. The accessory glands of reproduction comprise a relatively large, disseminate prostate, which surrounds the prostatic urethra immediately below the bladder and drains into it via numerous prostatic ducts. One or more pairs of Cowper's (bulbo-urethral) glands lie in close association with the crus of the penis. Each bulbo-urethral gland empties by a single duct into the membranous urethra close to its junction with the penile urethra. In contrast to eutherian mammals, marsupial reproductive systems lack seminal vesicles, ampullae and coagulating glands. The only apparent exceptions to this are found in the South American caenolestid, *Caenolestes obscurus*, (Rodger 1982) and the Mountain Pygmy-possum, *Burramys parvus* (Temple-Smith 1984a), where the distal portion of the vas deferens forms a convoluted secretory segment which resembles the eutherian ampulla.

In most marsupials, the scrotum develops postnatally (Kaiser 1931; McCrady 1938; Bolliger & Carrodus 1939, 1940; Hill & Hill 1955; Tyndale-Biscoe 1968; Guiler 1970b; Poole 1973; Setchell 1977) and testicular descent into the prepenile scrotum is usually complete at about 70–80 days postpartum (Finkel

1945; Maynes 1973; Turnbull, Mattner & Hughes 1981) although it requires only 25 days in the Eastern Barred Bandicoot, *Perameles gunnii* (Heinsohn 1966). The testes and epididymides of most adult marsupials are retained in a permanent scrotal position inside a pendulous scrotum (Biggers 1966; Setchell 1977; Temple-Smith 1984a; Tyndale-Biscoe & Renfree 1987) which is attached to the ventral body wall by a thin stalk carrying the spermatic cord. In the Thylacine, *Thylacinus cynocephalus* (Pocock 1926), and the Water Opossum, *Chironectes minimus*, the scrotum lies inside a pouch-like skin fold. In the Southern Hairy-nosed Wombat, *Lasiorhinus latifrons*, the testes are carried in a small non-pendulous scrotum (Brooks, Gaughwin & Mann 1978). In the fossorial Marsupial Mole, the testes are permanently abdominal or inguinal (Sweet 1907; Johnson 1983) as in eutherian moles. Whereas *Notoryctes* is the only testicondid marsupial, this condition is more widespread in eutherian groups, for example, in elephants, hyraxes, most edentates, marine mammals and some insectivores (Bedford 1977).

Distribution of scrotal hair varies in marsupial species and may show a correlation with environmental factors such as temperature and humidity. In phalangerids, for example, scrotal hair is absent in some tropical species, such as the Scaly-tailed Possum, *Wyulda squamicaudata*, (Burbidge 1983) whereas in many of the southern temperate species such as the Petauridae Common Ringtail Possum, *Pseudocheirus peregrinus*, Greater Glider, *Petauroides volans*, members of the Burramyidae and the Honey Possum, *Tarsipes rostratus*, the scrotal skin is more densely furred (Temple-Smith 1984a). In the dasyurid Brown Antechinus the scrotum is thickly furred in reproductive males, but becomes naked and heavily pigmented in post-reproductive individuals (Woolley 1966a, 1966b). Pigmentation of the tunica vaginalis, a fibrous inner membrane which encloses the scrotal contents, has been observed in various Australian and American marsupial species (Biggers 1966; Finkel 1945; Rodger 1982; Setchell 1977; Temple-Smith 1984a).

Perhaps the most dramatic example of scrotal pigmentation is seen in *Tarsipes*, where the entire tunica vaginalis of sexually mature adult males is heavily and evenly pigmented over both the testis and epididymis (Cummins, Temple-Smith, & Renfree 1986; see also Tarsipedidae Chapter 33). Even in closely related species, living under apparently similar conditions, variations do occur in the incidence of tunical pigmentation. For example, in the Burramyidae the tunica vaginalis is pigmented in at least two species of the genus *Cercartetus*, but is unpigmented in the Mountain Pygmy-possum, *Burramys parvus*, and the Feathertail Glider, *Acrobates pygmaeus* (Temple-Smith 1984a). Similar examples can be found in the macropodids (see Chapter 29) and in American marsupials. The function of scrotal pigmentation remains a subject for speculation (Biggers 1966; Rodger 1982; Temple- Smith 1984a).

As in all scrotal mammals, the spermatic cord in marsupials is covered by a thick cremaster muscle, which transmits the vas deferens to the pelvic cavity and contains the vascular supply to and lymphatic drainage from the scrotal contents (Barnett & Brazenor 1958; Heddle & Guiler 1970; Lee & O'Shea 1977). In almost all marsupials, scrotal temperature is apparently regulated by a rete mirabile. The temperature differential between testicular and body temperatures varies from 1.4°C (*Didelphis albiventris*) to about 6.5°C (Common Brushtail Possum). In high ambient temperatures, the Brushtail Possum is able to increase this differential to about 14°C by scrotal licking (Carrick 1969).

Testicular structure and function

The marsupial testis is ellipsoidal and, like other mammals, consists of numerous long loops of convoluted seminiferous tubules separated by varying amounts of interstitial tissue, enclosed in a thick tunica albuginea (Setchell

1977; Temple-Smith 1984a; Tyndale-Biscoe & Renfree 1987). In the Dasyuridae, the testis contains from one to four seminiferous tubule loops (Woolley 1975). Seminiferous tubule diameters in dasyurids are extremely large (360–510 µm; Woolley 1975). In most other marsupials, with the exception of the bandicoots (Benda 1906b; Setchell 1977) and *Tarsipes*, tubule diameter rarely exceeds 300 µm (Setchell 1977).

The cell types and cellular organisation of the spermatogenic epithelium are typically mammalian in all species examined, as are the cellular changes which occur during the early stages of spermatogenesis up to the formation of the early spermatids. Spermiogenesis, the process by which round spermatids are moulded into the definitive sperm shape, is a more complex process in marsupials. This process has been described in detail only for bandicoots of the genus *Isoodon* (Sapsford & Rae 1969; Sapsford, Rae & Cleland 1967, 1969a, 1969b, 1970), *Trichosurus* (Harding, Carrick & Shorey 1976b), the Koala (Harding 1979), *Tarsipes* (Harding *et al*. 1982) and some American species (Phillips 1970; Rattner 1972).

The early stage of spermiogenesis and development of the flagellum in marsupials is generally similar to those described in eutherian mammals. Later stages differ markedly, especially in the condensation and shaping of the nucleus, development of the acrosome and the changing orientation of the sperm head. In most marsupials, chromatin condensation and nuclear flattening occur at right angles to the axis of the developing flagellum and the acrosome initially develops on the albuminal surface of the condensing nucleus (Sapsford *et al*. 1969a; Rattner 1972; Harding *et al*. 1976b). During this stage, a dense nuclear ring forms around the periphery of the developing acrosome and nucleus. Subsequently, the nucleus is rotated to a position parallel to the axis of the developing flagellum. Just prior to their release from the Sertoli cells, spermatozoa undergo a second nuclear rotation such that the immature spermatozoon is arranged again with its nucleus approximately at right angles to the long axis of the flagellum. By contrast, in the Koala and probably in wombats, nuclear rotation does not occur during spermatogenesis (Harding 1977).

The kinetics of spermatogenesis have been described for only a few marsupials (Setchell & Carrick 1973; Setchell 1977; see also Chapter 29). Eight stages in the spermatogenic cycle, with cellular associations similar to those found in eutherian species (Clermont 1972), have been described in the Red-necked Wallaby, *Macropus rufogriseus*, the Tammar Wallaby and the Common Brushtail Possum (Setchell & Carrick 1973) and in two species of bandicoot (Sapsford *et al*. 1967, 1969b; Mason & Blackshaw 1973;). The frequency with which these stages occur and their durations, was consistent within individuals and similar to eutherian species. Ten stages have been reported in the spermatogenic cycle of the opossum *Didelphis azurae* (Orsi & Ferreira 1978). Perhaps the most unusual spermatogenic cycle in marsupials has been observed in some species of small dasyurids, for example, the Brown Antechinus and the Swamp Antechinus, *Antechinus minimus* (Woolley 1966b, 1975; Kerr & Hedger 1983; Wilson & Bourne 1984). Males of these species live for only about 11 months before a post-mating die-off (see Dasyuridae Chapter 21) and have a single cycle of spermatogenesis followed by loss of all germ cell components of the seminiferous epithelium except for small numbers of sparsely distributed spermatogonia.

Few observations have been made of testicular enzymes in marsupials, though a testicular-specific lactate dehydrogenase isoenzyme has been identified in various species (Baldwin & Temple-Smith 1973; Holmes, Cooper & Vanderberg 1973). Its absence in prepubertal testes of Brushtail Possums suggests that the appearance of this isoenzyme is related to the onset of sexual maturity. This suggestion is supported by a study of seasonal activity in the Greater Glider which shows a direct correlation between onset of spermatogenic activity and

synthesis of testis-specific LDH isoenzymes (Baldwin, Temple-Smith & Tidemann 1974). A similar seasonal expression of LDH genes also has been described in some eutherian species (Blanco *et al.* 1969; Gutierrez *et al.* 1972).

As in some eutherian mammals, cyclical changes in metabolic activity of the Sertoli cells, manifested in the abundance and configuration of endoplasmic reticulum and the quantity of intracellular lipids during the spermatogenic cycle have been described in the Long-nosed Bandicoot, *Perameles nasuta* (Sapsford *et al.* 1969a, 1969b).

The structure and function of the interstitial tissue in marsupials are also like that of eutherians. In mature active testes of all marsupials (Duesberg 1920; Christensen & Fawcett 1961; Green 1963b; Gilmore 1969; Baldwin *et al.* 1974; Rodger 1982; Kerr & Hedger 1983; Fletcher 1985), Leydig cells are prominent in the interstitial tissue in association with peritubular myoepithelial cells, fibroblasts and occasional macrophages. The vascular supply and lymphatic drainage of the testis is also located in the interstitial space (Setchell 1977; Temple-Smith 1984a). Of the three types of interstitial organisation recognised in mammals (Fawcett, Neaves & Flores 1973) a Type 2 organisation, with Leydig cells occupying 5% or less of total testicular volume, is found in the Phalangeridae, Macropodidae and Microbiotheriidae (Setchell 1977; P.D. Temple-Smith unpublished data) and Type 3, characterised by large aggregates of Leydig cells occupying up to 20% or more of testicular volume, occurs in the Didelphidae and Caenolestidae (Rodger 1982), and Peramelidae (Setchell 1977). The functional significance or phylogenetic implications of these different interstitial morphologies are unknown.

The Leydig cells of marsupials are typical steroid-secreting cells with large concentrations of smooth endoplasmic reticulum, abundant mitochondria and lipid droplets (Christensen & Fawcett 1961; Temple-Smith 1984a).

The *in vitro* capacity of marsupial testicular tissue to synthesise androgens from a variety of steroid precursors has been shown in *Didelphis* (Cook *et al.* 1974). Testosterone synthesis was also elicited by LH stimulation *in vitro* and *in vivo* by LH injections three days prior to tissue incubation. George, Hodgins & Wilson (1985) demonstrated endocrine function in testes from pouch young of the Virginia Opossum 10 days post-natally, which coincided with scrotal formation. Testicular tissue was capable of testosterone synthesis in advance of the differentiation of the urogenital tract.

In vivo studies confirm the capacity of the testis in various marsupials to produce androgen (Carrick & Cox 1973; Cook, McDonald, & Gibson 1978; Lincoln 1978; Allen & Bradshaw 1980; Curlewis & Stone 1985a). Carrick & Cox (1973) measured testosterone and, in some species, 5a-DHT levels in testicular vein plasma from five Australian marsupials and found similar androgen levels to those of some eutherians (Setchell 1977). The rate and control of androgen secretion from marsupial testes resemble that of eutherian species. Lincoln (1978) increased testosterone concentration in peripheral blood by *in vivo* injection of Gn-RH in five macropodid species.

The secretion and composition of fluid from the metatherian testis has only been examined in the Tammar Wallaby (see Chapter 29 this volume).

Sperm production by the testis has been estimated in a variety of Australian and American species using a histological assessment (Bedford, Rodger & Breed 1984). These studies showed a very low sperm production by the testis in didelphids, caenolestids, dasyurids and peramelids, but a much higher sperm production, within the eutherian range, in macropodids and phalangerids. Estimating from the data of Setchell (1970), the normal rate of sperm production by the Tammar Wallaby is about 500 million sperm per day. Recent estimates of sperm production in the didelphid, *Monodelphis domesticus*, of between

0.3-1.5 million sperm per day (P.D. Temple-Smith, L. Baggott & H.D.M. Moore unpublished data), are more than two orders of magnitude less than the values for the Tammar Wallaby.

Rete testis, efferent ducts and epididymis

The rete testis has two basic forms in marsupials (Setchell 1977; Rodger 1982; Woolley 1975, 1987). In didelphids, caenolestids, dasyurids and probably peramelids it develops in the centre of the testicular parenchyma. In macropodids and phalangerids, however, it forms a horseshoe-shaped structure beneath the tunica vaginalis about half way along the testis from the hilum and directly under the testicular vasculature (Setchell 1970).

The epididymis is linked to the testis by the ductuli efferentes which are comparatively long and straight and, as in eutherian mammals (Mason & Shaver 1952; Martan, Hruban & Slesers 1967; Hamilton 1972, 1975), absorb most of the fluid secreted by the testis. In most marsupials the efferent duct also forms a convoluted segment in the proximal segment of the caput epididymidis (Ladman 1967; Martan *et al*. 1967; Rodger 1982). There appears to be a correlation between testicular size and the number of efferent ducts draining to the epididymis. In *Didelphis* (Ladman 1967), the Phascolarctidae and larger species of phalangerids, macropodids and peramelids, up to 15 efferent ducts leave the testis whereas in the smaller species in these groups and the Dasyuridae (Woolley 1975; Fletcher 1985) and Caenolestidae (Rodger 1982) a single efferent duct passes in the mesorchial fold to the epididymis.

The marsupial epididymis, while showing some diversity in size, shape and structure of the duct (Setchell 1977; Rodger 1982; Jones, Hinds & Tyndale-Biscoe 1984; Temple-Smith 1984a, 1984b) is usually divisible into the three regions found in other mammals: caput, corpus and cauda, responsible for absorption, sperm maturation and sperm storage, respectively (Setchell 1977; Cummins 1981; Rodger 1982; Jones *et al*. 1984; Temple-Smith 1984a; Cummins *et al*. 1986). In representatives of the Phalangeridae (Temple-Smith 1984b), Macropodidae (Jones *et al*. 1984) and Tarsipedidae (Cummins *et al*. 1986) the epididymis has a specialised zone of phagocytic principal cells which selectively remove sperm cytoplasmic droplets from the lumen of the duct. In some dasyurids (Harding *et al*. 1982; Taggart & Temple-Smith 1985) the caudal epithelium is irregular and lined by an unusual and dense array of short microvilli on its luminal surface. In some species, in particular, didelphids and dasyurids, the caudal sperm storage capacity of the epididymis appears limited to only a few million spermatozoa (Bedford *et al*. 1984). The epididymides are connected to the prostatic urethra by the vasa deferentia which in some species (Rodger 1982; Temple-Smith 1984a) are specialised at their prostatic ends to form enlarged, highly coiled segments lined by tall columnar secretory cells. In appearance these segments resemble the eutherian ampulla.

Accessory glands

In contrast to most eutherians, the accessory glands of reproduction in marsupials consist only of prostate and bulbo-urethral glands. The metatherian prostate is proportionately larger than its eutherian equivalent and at times of peak secretory activity is one of the largest glandular structures in the body (Bolliger 1946; Gilmore 1969; Rodger & Hughes 1973), perhaps reflecting its major role in providing fluid components for the ejaculate.

The marsupial prostate is disseminate in structure, with glandular tissue confined between the lining of the prostatic urethra and the outer urethral muscle layer. It consists of numerous simple branching tubules lined by a columnar secretory epithelium which varies in height in each gland segment

(Rodger & Hughes 1973) and between species. Secretory tubules are arranged radially and empty into the urethra via a series of collecting ducts, which form a distinct central zone around the urethra. The outer layer of muscle which ensheaths the prostatic tissue presumably provides the motive force to express prostatic secretions at ejaculation.

A carrot-shaped prostate is found in the Macropodidae, Dasyuridae, Thylacinidae, Tarsipedidae, Petauridae, Phalangeridae, Notoryctidae and in the Southern Hairy-nosed Wombat. A heart-shaped prostate occurs in the Peramelidae and Phascolarctidae (Rodger & Hughes 1973). The prostate of the caenolestid, *Caenolestes obscurus*, is segmented like a didelphid (see below), but appears similar to the heart-shaped peramelid prostate (Rodger 1982). Within the Burramyidae, all *Cercartetus* species and the Mountain Pygmy-possum have a carrot-shaped prostate (Temple-Smith 1984a), whereas the Feathertail Glider has a distinctly heart-shaped organ with a long membranous urethral segment as in peramelids and the Koala (Ward, S.J. & Renfree, M.B. unpublished data). The didelphid marsupials appear to possess a carrot-like prostate which lies in the pelvic cavity in a distinct S-shape.

Histological segmentation of the prostate has been examined in detail in various marsupials and distinct regions have been defined which show some variation between, and sometimes within, family groups. In the Macropodidae, Burramyidae, Tarsipedidae and in some phalangerids and didelphids, two or three well-defined transversely oriented segments (anterior, central and posterior) can be distinguished both structurally and biochemically (Chase 1939; Rodger & Hughes 1973; Nogueira, Ribeiro & Campos 1985). By contrast, prostates of the Dasyuridae and the Common Ringtail Possum are subdivided longitudinally into superficial and deep posterior segments and the peramelid prostate comprises distinct dorsal and ventral components (Rodger & Hughes 1973). Neutral or acid mucosubstances, proteins and lipids are the major secretory products of the metatherian prostate. In contrast to most eutherian mammals, fructose is absent or virtually absent from prostatic tissues, except in the Southern Hairy-nosed Wombat, but glucose and zinc concentrations are similar to those in some eutherians (Rodger & White 1974a, 1974b; Cook *et al*. 1978). In many Australian marsupials, N-acetyl glucosamine replaces fructose as the major free sugar in seminal plasma (Rodger & White 1976). In macropodids and phalangerids, N-acetylglucosamine is derived from the central segment and in peramelids from both prostatic segments. The functional importance of this sugar in seminal plasma remains to be explained. In the Didelphidae and Dasyuridae high concentrations of glycogens are found, especially in the posterior segment (Martan & Allan 1965; Rodger & White 1980; Nogueira *et al*. 1985).

Bulbo-urethral glands occur in all metatherians but little is known about their structure or functions. One to three pairs are found in Australian marsupials (Rodger & Hughes 1973; Woolley & Webb 1977; Smith 1984a, 1984b; Temple-Smith 1984a; Fletcher 1985) and three pairs occur in all didelphid marsupials which have been examined (Chase 1939; Ribeiro & Noguiera 1982; Nogueira, Campos & Ribeiro 1984). These glands lie adjacent to the crura of the penis and urethral bulbs, are usually partially enveloped in a sheath of striated muscle and empty into the urethra via narrow ducts. The secretion contains neutral mucosubstances, and varying amounts of protein and lipid (Rodger & Hughes 1973). Acidic mucosubstances, for example sialo- and sulphomucins are also elaborated by some species (Rodger & Hughes 1973; Noguiera *et al*. 1984) and also glycogen (Noguiera *et al*. 1984). The function of this secretion may be simply to lubricate the urethra prior to ejaculation.

Metatherian accessory glands appear to be androgen-dependent and in all seasonal breeders, hypertrophy of these glands coincides with the breeding season and peak plasma levels of androgens (Woolley 1966a, 1966b; Cook *et al*. 1978; Inns 1982; Kerr & Hedger 1983; Wilson & Bourne 1984; Fletcher 1985).

Seasonal control of prostatic hypertrophy in the Common Brushtail Possum may occur by direct transfer of androgens from the reproductive tract secretions, which pass into the prostatic urethra distal to the openings of the ductus deferens, via the rich vascular plexus in this region. The positive correlation observed between serum testosterone concentration and prostatic weight (Cook *et al*. 1978) may suggest that peripheral levels of circulating androgens also exert a direct control over prostatic function in this species.

Penis

The penis in marsupials is usually internalised as a sigmoid-shaped structure inside the preputial sac in the cloaca (Biggers 1966; Rotenberg 1928; Woolley & Webb 1977; Young 1879). It usually is extruded only during sexual interactions and in many species is difficult to externalise outside the breeding season. In most marsupials the glans penis is a prominent, bifurcated structure, although various extreme and intermediate forms exist (Biggers 1966). The most prominently bifid penis is found in various American marsupial genera, for example, *Caluromys*, *Didelphis*, *Marmosa* and *Caenolestes* (Biggers 1966; Osgood 1921). In all these species the urethra does not pass through the glans, but extends as a groove along the medial surface of each half. At the other extreme, there is apparently no glans in *Tarsipes* (Rotenberg 1928) and in macropodids, the glans remains united as a single filiform structure. In the Bilby the penis and urethra are bifurcated and the urethra extends throughout its length in the substance of the glans (Owen 1868). In addition to a penile bifurcation, some dasyurids possess an accessory erectile body associated with the penis and derived from the corpora cavernosa (Woolley & Webb 1977).

Penile morphology has been successfully used as a taxonomic character in some marsupial groups. For example, Woolley & Webb (1977) and Woolley (1982a) distinguished two major groupings of small dasyurids on this basis.

Sperm structure and maturation. Sperm structure in marsupials has been extensively studied and some information is now available on all extant families (except the Notoryctidae) and a large number of genera (Hughes 1965; Biggers 1966; Phillips 1970; Harding, Carrick & Shorey 1975, 1976a, 1976b, 1979, 1984; Harding *et al* 1982; Cummins 1976; Olson & Hamilton 1976; Temple-Smith & Bedford 1976, 1980; Olson *et al*. 1977; Temple-Smith 1984a; Temple-Smith & Grant 1987). Considerable variation in sperm structure, which has useful phylogenetic implications, occurs between families of the Metatheria although a general conservation of structure is found within families (Fig. 17.14) (Hughes 1965; Biggers 1966; Harding *et al*. 1979, 1984; Harding, Carrick & Shorey 1981c; Harding *et al*. 1982; Temple-Smith 1984a; Temple-Smith & Grant 1987).

The components of sperm structure are the same as in eutherians, but the structural arrangement of these components differs from the general eutherian pattern. In nearly all Australian marsupials the nucleus usually forms an elongated cone or wedge, often dorso-ventrally compressed, with a prominent funnel-shaped invagination on its ventral surface which narrows anteriorly (Fig. 17.14; see also Temple-Smith 1984a). This receives the elongated connecting piece of the flagellum which usually articulates with the nucleus at the anterior extremity of the ventral cleft (Fig. 17.14). The only significant variations from this in Australian species are seen in the hook-shaped sperm head and eutherian-like articulation between the nucleus and flagellum in the Koala and Wombats (Harding *et al*. 1979; Hughes 1965, 1977b) and also the

more irregularly shaped nucleus of the peramelids (Hughes 1965; Sapsford *et al.* 1969a). Considerably more variation is seen in American marsupial families (Fig. 17.14) (Temple-Smith & Grant 1987). Except in the Microbiotheridae, such variation is further complicated by sperm pairing (Biggers 1966; Phillips 1970; Temple-Smith & Bedford 1980; Temple-Smith & Grant 1987). This process occurs during sperm maturation in the epididymis and results in a precise head-to-head association between pairs of sperm across their acrosomal surfaces (Fig. 17.14) which appears to be maintained by a perinuclear 'gap' junction between adjacent plasma membranes (Phillips 1970; Temple-Smith & Bedford 1980). Sperm head structure in the Microbiotheridae closely resembles that described in Australian species (Fig. 17.14) perhaps suggesting a close phylogenetic association between these groups (Temple-Smith & Grant 1987). The flagellum contains the usual 9 + 2 axonemal complex surrounded by nine dense fibres and is divided into mid- and principal pieces by a prominent annulus. A dense sheath of mitochondria characterises the mid-piece and, in all species examined so far except the Koala (Harding *et al.* 1979), a helically arranged network of fibres beneath the plasma membrane is found in the posterior region of the mid-piece, sometimes in association with flask-like membrane invaginations (Harding *et al.* 1975, 1979; Olson 1975; Temple-Smith & Bedford 1976; Temple-Smith & Grant 1987).

In Australian marsupials, sperm size varies considerably (Cummins & Woodall 1985), ranging from about 90–120 µm in the Phascolarctidae, Vombatidae, Macropodidae, Phalangeridae, Burramyidae and Petauridae, 170–200 µm in the Peramelidae and 200–250 µm in the Dasyuridae. The largest mammalian sperm is found in the diminutive Honey Possum (350 µm).
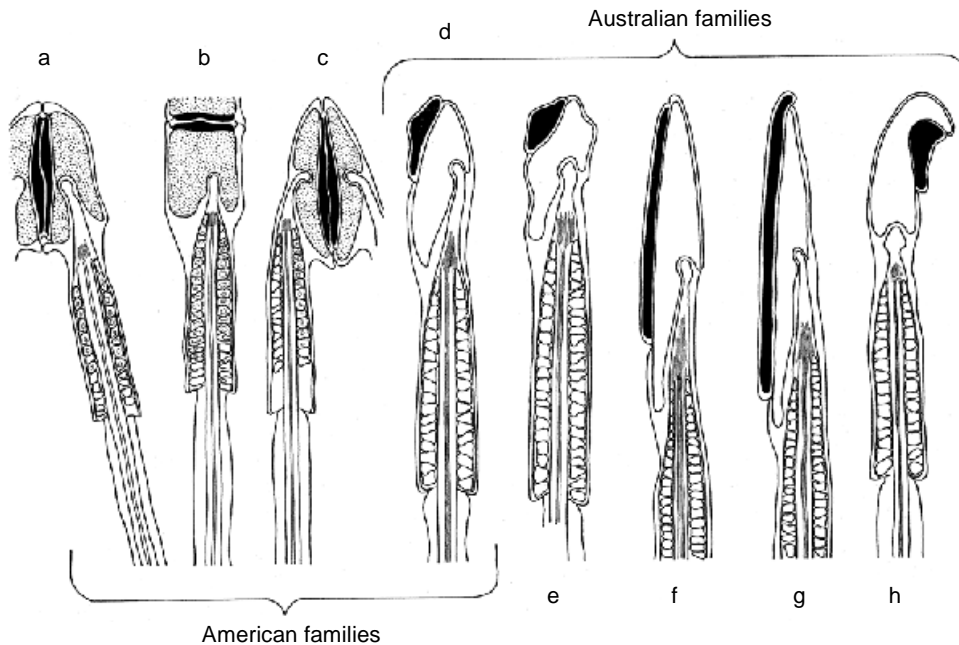

Figure 17.14 Comparison of the basic structural features of the head and midpiece of Australian and American marsupial spermatozoa. Note the occurrence of sperm pairing in American marsupial families and the distinct family-specific nuclear shapes. (a) Didelphidae; (b) Caenolestidea; (c) Caluromyidae; (d) Microbiotheridae, Phalangeridae, Petauridae, Burramyidae, Macropodidae; (e) Peramelidae; (f) Dasyuridae; (g) Tarsipedidae; (h) Phascolarctidae, Vombatidae. (Redrawn from Temple-Smith & Grant 1987; P.D. Temple-Smith unpublished; Hughes 1965, 1977c; Harding *et al.* 1979, 1982). [K. Hollis]

Sperm maturation is a distinctive process. In addition to development of progressive motility during passage through the epididymis (Cummins 1976, 1977; Temple-Smith & Bedford 1976, 1980), marsupial spermatozoa undergo a series of complex structural changes during the maturation process (Harding *et al*. 1975, 1979, 1982; Temple-Smith & Bedford 1976, 1980; Olson & Hamilton 1976; Temple-Smith & Grant 1987). Most or all of such changes during sperm maturation occur in all species so far examined with the exception of the Koala (Hughes 1965, 1977b; Harding *et al*. 1979).

Seasonal effects on male reproduction

Few detailed studies have been made on seasonal effects in male marsupials, whereas there is an extensive body of data of the effects of season on reproduction in females, especially the Macropodidae (Biggers 1966; Tyndale-Biscoe 1984a for reviews; and see Chapter 29). As assessed by constant testicular size and continuing spermatogenesis, a large number of species shows no seasonality in male reproduction. These include various large central American didelphids (Biggers 1966), most macropodids (Hughes 1964; Sadleir 1965; Catt 1977; Inns 1982), *Tarsipes* (Scarlett & Woolley 1980; Renfree, Russell & Wooler 1984), the Common Brushtail Possum (Gilmore 1969), the Northern Brown Bandicoot, *Isoodon macrourus* (Gemmell, Johnson & Barnes 1985) and the Common Wombat, *Vombatus ursinus* (Hughes 1964). Although spermatogenesis is continuous in this group, seasonal changes in prostatic size and in plasma concentrations of testosterone, LH and FSH have been observed. These have been linked to seasonal environmental effects (Gilmore 1969; Catt 1977; Inns 1982; Gemmell *et al*. 1985) or, in the Tammar Wallaby, to a seasonal stimulatory effect of oestrous females (Catling & Sutherland 1980; see Chapter 29 this volume).

Many other species are obligate seasonal breeders which undergo seasonal involution of the entire reproductive tract and cessation of spermatogenesis. These include dasyurids (Sharman 1959; Godfrey 1969b; Fletcher 1985), burramyids (Ward & Renfree 1986), petaurids (Smith 1969; Baldwin *et al*. 1974) and pseudocheirids (Hughes, Thomson & Owen 1965). Species of *Antechinus* provide an intermediate situation, in which the testis has a single spermatogenic cycle followed by complete loss of germ cells from the seminiferous tubules (Kerr & Hedger 1983). In these species, the interstitial component continues to generate testosterone and the remaining elements of the reproductive tract remain actively enlarged until male die-off occurs (Woolley 1966a, 1966b; Kerr & Hedger 1983; Wilson & Bourne 1984).

Breeding biology, oestrus cycles and pregnancy

Most marsupials are seasonal breeders and produce relatively small young ranging from less than 5 mg to no more than one gram. Although the maternal investment in pregnancy is very small and much less than that of eutherian mammals, a major investment is made during the long period of lactation. In most marsupials, either ovulation or post- blastocyst development is prevented by the presence of suckling pouch young. Once the breeding season ends, however, the absence of the pouch young usually results in the animals becoming either anoestrus or quiescent. The shortest gestation period is 12.5 days (in the Peramelidae) and the longest is 36 days in the Eastern Grey Kangaroo. Detailed tables of the breeding biology of marsupials are provided in the extensive review of Tyndale-Biscoe (1984a) and in Tyndale-Biscoe & Renfree (1987).

The pattern of the oestrous cycle, including histological changes in the uterus and ovary during the follicular and luteal phases bears many similarities to the patterns in the Eutheria (Pilton & Sharman 1962; Sharman & Berger 1969).

Many of the steroid hormones and gonadotropins involved in reproduction in eutherian mammals have been found in marsupials, though particular features of their functions differ (Tyndale-Biscoe & Renfree 1987). Ovulation is spontaneous in all marsupials and in most species occurs within 2 days of oestrus.

Marsupials may be monoestrous, but the majority are polyoestrous. The marsupial oestrous cycle varies in mean length from 22–42 days, the average being 28 days (Tyndale-Biscoe 1973). The life of the corpus luteum is not prolonged by the presence of a conceptus, although in the Peramelidae, the corpus luteum persists during lactation (Hughes 1962b; Gemmell 1981). Because pregnancy is shorter than the oestrous cycle in all except in the Swamp Wallaby, *Wallabia bicolor*, the young are born, depending on the species, at different stages of the luteal and follicular cycle. The timing of birth and oestrus has been altered experimentally in the Red Kangaroo, suggesting that gestation and oestrous cycle activity need not be closely linked (Clark 1968).

In the American opossums *Didelphis virginiana* and *Marmosa mitis*, as in many monovular and polyovular Australian species, the young are born toward the end of the luteal phase, and the return to oestrus is suppressed by the suckling stimulus. In contrast, in the macropodids the single pouch young reaches the pouch at the end of the pro-oestrous phase, and ovulation and fertilisation occur postpartum (Fig. 17.15). Embryonic diapause in the Macropodidae is discussed in Chapter 29.
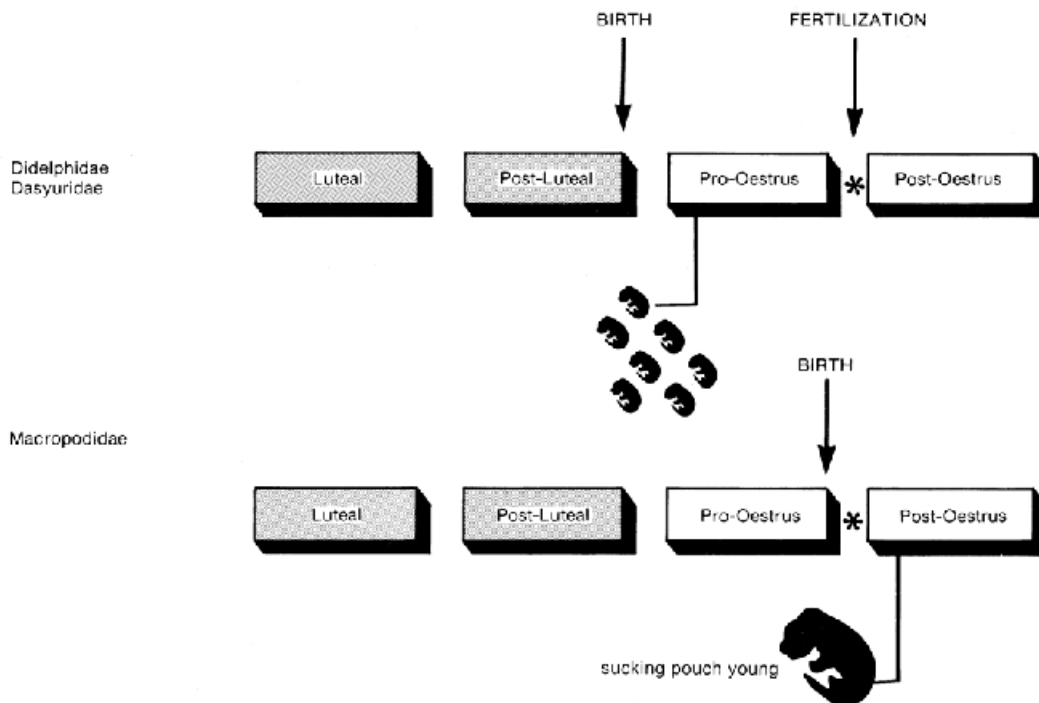

Figure 17.15 Marsupial oestrous cycles. In species such as the American opossums (Didelphidae) or the Australian dasyurids (Dasyuridae) (top), birth occurs toward the end of the uterine luteal (secretory) phase and the presence of the numerous young in the pouch prevents the pro-oestrous phase and the development of the follicle. Should the young be lost, animals return to oestrus. By contrast, in the macropodids (bottom), gestation occupies the whole length of the oestrous cycle and ovulation occurs within a day after the birth of the single young. Sucking of the teat by the pouch young prevents development of the embryo beyond the blastocyst stage. * indicates ovulation and fertilisation. (After Renfree 1980a)

Marsupial reproductive strategies are divisible into two, or possibly three, main groups (Tyndale-Biscoe 1984a). Group 1 recently has been further subdivided in two groups to accommodate the peramelids (Tyndale-Biscoe & Renfree 1987) so identifying four different reproductive strategies:

a) polytocous or monotocous polyoestrous species in which the gestation period is considerably shorter than oestrus cycle and postpartum oestrus ovulations are suppressed during lactation. This pattern seems to be common to the Petauridae, Phalangeridae and to the majority of polyprotodont marsupials as well. Tyndale-Biscoe (1984a) concluded that it represents the basic marsupial pattern from which the other strategies have been derived. The evidence from Dasyuridae suggests that the monoestrus pattern of *Antechinus* and *Dasyurus* has been derived from a polyoestrous pattern as special adaptations of seasonal breeding. The Peramelidae also fits this pattern.

b) monotocous, polyoestrous species in which the gestation period is almost the same length as the cycle, so that post-partum oestrus and ovulation occur. During lactation, further development is arrested and if fertilisation occurs, the embryo remains as a unilaminar blastocyst of about 100 cells in embryonic diapause. Most of the Macropodidae share this pattern.

c) polytocous or monotocous polyoestrous species in which the gestation period is almost the same length as the cycles, so that post-partum oestrus and ovulation occur; arrest of further development is not lactation-controlled, but may be seasonally controlled. It is possible that the Honey Possum (Renfree 1981) and the Feathertail Glider (Ward & Renfree 1986) may share this distinctly different pattern.

Mammary glands and lactation

Lactation in marsupials lasts for relatively longer than in most eutherian species, to support young which are more immature at birth (Tyndale-Biscoe, Stewart & Hinds 1984). The newborn marsupial climbs, unaided by the mother, into the pouch where it spends a considerable period sustained by the specialised milk which changes in composition as the young grows. Pouch young remain permanently attached for about the first half of the period spent in the pouch and are totally dependent on milk until weaning. Three broad stages in lactation have been described: preparation of the mammary gland, initiation and maintenance of lactation during the first, dependent phase of pouch life and maintenance of an increased milk production during the later, rapid growth phase (Findlay & Renfree 1984; Tyndale-Biscoe *et al*. 1984). The number of teats generally limits the number of young that can survive in polyovular species like dasyurids, but many species have supernumerary nipples. In all Macropodidae and Phalangeridae, for example, there is a choice of four teats for the single pouch young (Fig. 17.16). Extensive reviews on marsupial milk composition, mammary gland structure and the physiology of lactation were provided by Findlay & Renfree (1984), Green (1984), Tyndale-Biscoe *et al*. (1984) and Tyndale-Biscoe & Renfree (1987).

Relatively few experiments have been reported on the physiology of lactation, almost all of them on macropodid species (see Chapter 29) although one of the usual features of lactation in marsupials is the constantly altering composition of the milk. As in all mammals, the first milk is a colostral type secretion, a clear, low-fat fluid with free floating cells (Griffiths, McIntosh & Leckie 1972). Immunoglobulin γ- and α-like proteins have been identified in the colostral milk of opossums (Virginia Opossum) and in the neonatal serum within 12 hours of birth, but not in newborn, unsuckled opossums (Hindes & Mizell 1976). This is in contrast to the Tammar Wallaby, in which immunoglobulins were detected in serum of fetuses from day 24 onwards of the 27 days gestation and from

Figure 17.16 The pouch of a Tammar Wallaby, showing the four teats (arrowed) which are characteristic of macropodids and a small pouch young attached to one teat. Note the enlarged teat which is still being used by a young-at-foot. (© ABRS)

unsuckled neonates (E. Deane, D.W. Cooper & M.B. Renfree unpublished data; Renfree 1973). Immunoglobulins form an important component of later marsupial milks. The pouch young passively acquire antibodies from the milk by uptake through the gut (Yadav 1971; Bell, Stephens & Turner 1974).

The main constituents of marsupial milk are similar to those of eutherian mammals, but there are marked changes throughout lactation (Fig. 17.17) corresponding with changes in the sucking regime of the pouch young from continuous to intermittent (Green, Newgrain & Merchant 1980; Green 1984). Total solids are higher than in cow or human milk; proteins, carbohydrates and fats increase quantitatively and change qualitatively during lactation (Jenness 1974; Messer & Green 1979). Both caseins and whey proteins are found, but the latter have been better studied and show the greatest variation (Bailey & Lemon 1966; Lemon & Bailey 1966; Lemon & Barker 1967; Green & Renfree 1982).

The limited data available suggest that all marsupials have a similar pattern of milk composition, the relatively dilute milk produced to supply the new pouch young becoming progressively more concentrated (Green 1984). The mammary glands also increase in size throughout lactation (Findlay & Renfree 1984; Tyndale-Biscoe *et al*. 1984) and the growth rates of the young are regulated by rates of milk production and its changing composition (Green 1984). Although the cellular processes of embryological and pre- pubertal development and the proliferation and differentiation of the mammary glands during pregnancy are similar in all mammals, the temporal course of these events is different in marsupials (Findlay & Renfree 1984).

EMBRYOLOGY AND DEVELOPMENT

Ovulation and fertilisation

Ovulation is spontaneous in all marsupials adequately studied and in most species occurs within two days of oestrus: the Virginia Opossum (Hartman 1923), *Marmosa robinsoni* (Godfrey 1975), the Common Brushtail Possum (Pilton & Sharman 1962; Shorey & Hughes 1973), the Quokka (Sharman 1955a), the Tammar Wallaby (Tyndale-Biscoe & Rodger 1978). In only two

species is the interval from oestrus to ovulation much longer; in the Eastern Quoll it is 5 days (Hill & O'Donoghue 1913) and in the Brown Antechinus 10 days (Woolley 1966b). There are timed observations on the process of fertilisation in only three species: the Virginia Opossum (Rodger & Bedford 1982a, 1982b), the Tammar Wallaby (Tyndale-Biscoe & Rodger 1978) and the Brown Antechinus (Selwood 1982). Sperm transport is very rapid. Within an hour after copulation spermatozoa are either in the uteri, concentrated at both cervices, or entrapped in the semen and within the two cervical canals where the secretions frequently form a coagulum or copulatory plug (Hartman 1924; McCrady 1938; Tyndale-Biscoe & Rodger 1978).

Ovulation occurs about 10 hours after copulation in *Didelphis* and fertilised eggs are found in the oviducts about 5 hours later, with two-celled eggs in the uterus by 22 hours post-coitum (Rodger & Bedford 1982a, 1982b). Before fertilisation the paired spermatozoa separate from the anterior, acrosomal surface; only separated spermatozoa participate at fertilisation. Bedford *et al.* (1984) suggest that the pairing protects the acrosome because they attach to the zona by the acrosomal face.

With the second maturation division the second polar body is extruded in preparation for syngamy, either in the oviduct 26 hours after copulation (Rodger & Bedford 1982b) or in the uteri (Hartman 1916). The cortical granule release which accompanies fertilisation may provide a first block to polyspermy and the mucoid or albuminous coat, a secondary block, as in the rabbit (Aitken 1981). Eggs already covered by the mucoid coat would be impenetrable, possibly explaining the large number of unfertilised eggs in the Virginia Opossum (Rafferty-Machlis & Hartman 1953), the Tasmanian Devil (Hughes 1982a) and the Brown Antechinus (Selwood 1983).

In addition to the secondary membrane (zona pellucida) laid down in the developing follicle, all marsupials have a keratinous, tertiary membrane secreted by the epithelia of the oviduct and uterus, the 'shell' (Hughes 1977a) separated from the zona by a mucoid layer. The zona pellucida varies in thickness from about 1 µm in *Didelphis* to 6 µm in Brushtail Possums and the Tammar Wallaby and is thus considerably thinner than in eutherian mammals in which it is 10-30 µm thick (Tyndale-Biscoe & Renfree 1987). As the unilaminar blastocyst expands, the zona disappears (Hughes 1974).

The albumin or mucoid coat is secreted by the oviducal glands. Supernumerary spermatozoa become entrapped in it and remain there until its disappearance with the zona, when the blastocyst expands. The fully-formed mucoid coat varies in thickness in marsupials from less than 10 µm in *Perameles* to 230 µm in *Didelphis* (Tyndale-Biscoe & Renfree 1987).

The shell membrane is the homologue of the basal layer of the monotreme shell (Caldwell 1887; Hill 1910; Hartman 1916). The first trace of it is seen on eggs recovered from the utero-tubal junction, and deposition continues after the egg enters the uterus (Tyndale-Biscoe & Renfree 1987). The maximum thickness is seen on unilaminar blastocysts that have not expanded, and ranges from 1-1.6 µm in *Didelphis* to 10 µm in the Koala. It is a resistant proteinaceous substance, rich in disulphide bonds and with the histochemical properties of an ovokeratin (Hughes 1974), quite unlike the avian calcareous shell or its inner shell membrane. Its function is not clearly established, but its persistence for two-thirds of gestation in all marsupials examined (Hughes 1974) and its disappearance at the beginning of organogenesis may be significant (Tyndale-Biscoe & Renfree 1987).

Embryonic development

Cleavage and the formation of the blastocyst. The eggs of marsupials vary quite considerably in size (Tyndale-Biscoe & Renfree 1987). The ooplasm contains clear material and lipid droplets ('yolk'), as well as sub-cellular organelles (Lyne & Hollis 1976). In the Eastern Quoll, the yolk is segregated as a distinct body during the first and second cleavages (Hill 1910) and similarly in the Brown Antechinus by the second cleavage (Selwood 1983). In embryos of 30 cells or more, polarity is lost and the blastomeres are joined at their margins to form a unilaminar blastocyst of 60 cells. Up to this stage there has been no increase in the overall diameter of the embryo, but hereafter the blastocyst expands.

The eggs of the Virginia Opossum and *Didelphis marsupialis* are smaller than those of *Dasyurus* and *Antechinus*, the yolk is less abundant (Hartman 1916) and after fertilisation the latter is not concentrated at one pole. After the third and fourth cleavage divisions, yolk material is displaced to the centre and becomes enclosed within the early blastocyst.

There is very little information on cleavage and yolk extrusion in other marsupials (Tyndale-Biscoe & Renfree 1987). Hughes (1982a) illustrated cleavage stages in the Tasmanian Devil, which resemble those of *Dasyurus* and *Antechinus* and Lyne & Hollis (1976, 1977) examined 4-cell and 8-cell embryos recovered from the uteri of the Long-nosed Bandicoot. In the 4-cell stage, the blastomeres are equal in size and still connected to a central mass of yolk, like in the dasyurids.

Cleaving eggs have been illustrated for the diprotodont marsupials Brushtail Possums (Sharman 1961b; Hughes 1974), the Greater Glider (Bancroft 1973), the Tammar Wallaby (Renfree & Tyndale-Biscoe 1978; Tyndale-Biscoe 1979b) and the Eastern Grey Kangaroo (Tyndale-Biscoe & Renfree 1987). The blastomeres do not separate distinctly as in the dasyurids and separated yolk is not evident.

Marsupial eggs traverse the oviduct very rapidly, certainly in less than 48 hours and probably less than 24 hours, reaching the uterus before the first cleavage (Tyndale-Biscoe & Renfree 1987). By contrast, the first six cleavage divisions leading to formation of the unilaminar blastocyst are remarkably slow. Embryos that have undergone four or five cleavage divisions, are found on day 3 (Virginia Opossum, Long-nosed Bandicoot), day 4 or 5 (Common Brushtail Possum), day 6 (Brown Antechinus), day 7 (Tammar Wallaby, Eastern Quoll) and the fully formed unilaminar blastocyst on days 4, 5, 8, 8 and 9, respectively.

Thus, at the completion of the formation of the blastocyst, all marsupial embryos consist of a single layer of cells, the trophoblast, which forms the unilaminar blastocyst and in which no distinct polarity can be discerned. This is in contrast to most, but not all, eutherian blastocysts which have an outer trophoblast, readily distinguished from the cells which will eventually form the embryonic body, the inner cell mass (Fig. 17.18). Despite claims to the contrary (Lillegraven 1975, 1985), there is no evidence for a difference between these two mammalian trophoblasts (Tyndale-Biscoe & Renfree 1987) and the description of several eutherian mammals which also lack an inner cell mass at the blastocyst stage (see Wimsatt 1975; Fig. 17.18) attests to the homologies of this structure.

The bilaminar blastocyst. Up to the unilaminar blastocyst stage there is no increase in diameter. With the differentiation of endoderm mother cells in the trophoblast there is rapid expansion of the blastocyst through absorption of fluid into the blastocoele (Tyndale-Biscoe & Renfree 1987). The formation of the primary endoderm is similar in all species in which it has been described. The bilaminar blastocyst is complete at the end of day 6 in the Virginia Opossum, when the blastocyst is 0.74 mm diameter (McCrady 1938) and in blastocysts of
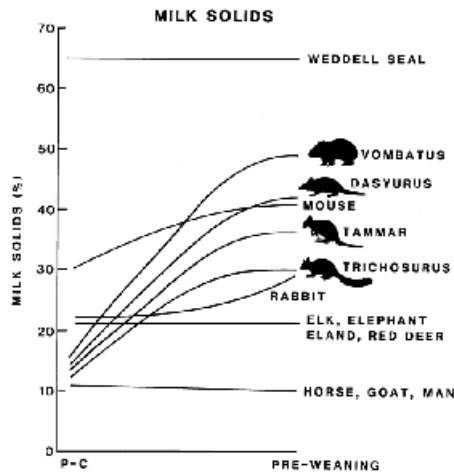
Figure 17.17 Diagrammatic comparison of the concentrations of milk solids throughout lactation in selected marsupials and eutherians. P-C = post-colostrum. (Redrawn from Green 1984; © ABRS)

the same size in *Bettongia* (Kerr 1935). In the Brown Antechinus, it is complete when the blastocyst is about 3.0 mm diameter at day 20 (Selwood 1980). The bilaminar blastocyst of the Eastern Quoll is 4.5–6.0 mm in diameter (Hill 1910) and this occurs on or about day 15 post-coitum or day 10 after ovulation. In bandicoots, the blastocysts are fully bilaminar when 1.5–1.9 mm (Hollis & Lyne 1977) and this is estimated to occur 6 days post-coitum (Lyne & Hollis 1977).

Post-blastocyst development of the embryo. Relatively few studies have described early intrauterine development of marsupials, for example, *Didelphis* (Selenka 1887; Hartman 1916, 1919, 1923, 1928) and only one (McCrady 1938) described the development from the unfertilised egg to pouch life. A feature of marsupial embryogenesis is the relatively slow growth of the blastocyst, the rate of embryonic development only increasing during the latter stages of pregnancy, when it may be compressed into a few days (Sharman 1959; Tyndale-Biscoe 1968; Renfree & Tyndale-Biscoe 1973a; Tyndale-Biscoe & Renfree 1987).

The medullary plate and primitive streak are formed by a compaction of cells with the completion of the endoderm (Kerr 1936; McCrady 1938). The medullary plate elongates into a pear shape and as the primitive streak lengthens and the primitive groove develops within it, the embryo acquires a bilateral symmetry, with Hensen's node at the anterior end (Tyndale-Biscoe & Renfree 1987). The primitive streak shortens anteriorly and at the same time the notochord and the medullary groove appear. The first somites appear as two slight condensations of the mesoderm beneath the medullary plate on either side of the central mesoderm-free strip (Renfree 1972a; McCrady 1938). The first somites are seen in embryos between 4–8 mm diameter; an 11 mm Tammar Wallaby vesicle had three somites (M.B. Renfree unpublished observation) whereas a 4.4 mm vesicle of a Greater Glider had two somites (Bancroft 1973).

Amniogenesis occurs relatively late in marsupials, soon after the appearance of somites, beginning with the anterior proamnion and then the tail amnion (Tyndale-Biscoe & Renfree 1987). In the opossum, the proamnion forms when the embryo has 7 to 12 somites (McCrady 1938), and the (somatopleuric) amniotic tailfold is evident at 20 to 25 somites (Selenka 1887; McCrady 1938). In the Greater Glider the proamnion and tail amnion could be seen in an embryo with 10 somites (Bancroft 1973), whereas an embryo of the Long-nosed Bandicoot with 15 somites lacked any distinct evidence of amniogenesis (Luckett 1977). In a 23 somite embryo (4.7 mm greatest length) of the Eastern Quoll, both amniotic folds were present, as in the Virginia Opossum (Luckett 1977). Amniotic head and tailfolds were similarly observed in 4.8 mm (greatest length) Quokkas (day 19), 4.0–5.0 mm Tammar Wallabies (day 17), 4.2 mm Red-necked Wallabies (day 18) and 5.4 mm *Pseudocheirus* embryos (Sharman 1961b; Renfree 1973; Walker & Rose 1981). The proamnion persists throughout

intrauterine life in opossums (Selenka 1887; McCrady 1938), but not in phalangerids and macropodids (Sharman 1961b; Renfree 1972a; Bancroft 1973).

Cervical flexure occurs when the embryo has about 18 to 20 somites and the neural tube is closed along most of the length of the embryo (Tyndale-Biscoe & Renfree 1987). The anlagen of the olfactory, optic and otic organs are differentiated. The heart tubes are fused and branchial pouches differentiated. The pharyngeal region shows the development of Rathke's pouch at the anterior end. Lung anlagen are also present and mesonephric as well as pronephric tubules are formed. This occurs at around days 23–24 post-fertilisation in *Antechinus* (Selwood 1980), days 9–10 in the Virginia Opossum (McCrady 1938), days 18–19 in the Tammar Wallaby (Renfree 1972a) and the Red- necked Wallaby (Walker & Rose 1981) and day 17 in the Quokka (Sharman 1961b; Tyndale-Biscoe 1963b; Wallace 1981 and unpublished observation).

The notochord is complete at day 10 in *Didelphis* (McCrady 1938), day 22 in *Antechinus* (Selwood 1980), days 18–19 in the Tammar Wallaby and the Red-necked Wallaby (Renfree 1972a; Walker & Rose 1981). Also at about this time the shell membrane ruptures and there is the possibility for direct apposition of the trophoblast to the uterine epithelium. Whereas all development up to this stage has been relatively slow and occupied two-thirds of the active gestation period, organogenesis is relatively rapid.

Organogenesis. The duration of organogenesis is quite similar for species of very different adult body sizes. Relatively few studies have been made so far on the development of particular organ systems of marsupials, for example, the Common Brushtail Possum (Parker 1917; Tribe 1918). The development of the urogenital system in marsupials, with special reference to Brushtail Possums is given in Buchanan & Fraser (1918) and Fraser (1919). Burns (1939) and Nelson (1944) described aspects of differentiation of sex in the Virginia Opossum and some stages of development of the embryo of the Greater Glider were described by Bancroft (1973), that of the Tammar Wallaby by Renfree (1972a) and of the Red-necked Wallaby by Walker & Rose (1981). The developing organs in the neonates and pouch young of the Macropodidae are discussed in Chapter 28. The neonatal marsupial (which weighs less than 0.5 g) has, by comparison with the eutherian neonate, a mixture of 'altricial' and 'precocial' features (Tyndale-Biscoe & Renfree 1987). At birth, the tiny, naked marsupial is able to climb to the pouch unassisted by the mother, using its well-developed forelimbs. Its lungs are functional, the nostrils are open and the olfactory centre of its brain is well developed. The mouth, tongue, and digestive system, including liver and pancreas, are sufficiently developed to cope with the change to a milk diet. By contrast, features such as the eyes, the hind limbs and the gonads remain undifferentiated; pouch and scrotum can be clearly seen only after about 10 days post-partum in macropodids. The mesonephric kidney remains functional for the first few days after birth; the metanephros is differentiated, but not immediately functional. Nevertheless, the entire period of differentiation is accomplished in a short period, preparing the neonate for its more lengthy stay in the pouch whilst the rest of development is completed. Despite the emphasis on lactation rather than gestation, marsupials are, like other mammals, dependent on a placenta for intra-uterine life.

Placental structure and function

One of the commonest misrepresentations about marsupials is that they lack a placenta (Tyndale-Biscoe & Renfree 1987). Marsupials, like many other mammalian and non- mammalian animals (including invertebrates; see Amoroso, Heap & Renfree 1980), do have a functional and physiologically efficient placenta (Fig. 17.19). Any mention of placental mammals must,

therefore, refer to both eutherians and marsupials and, albeit for a short period, also to the monotremes (Griffiths 1983). The well-vascularised yolk sac is usually in intimate association with the endometrium, so that the membranes apposed to the uterine wall consist of vascular and non-vascular portions of the yolk sac. Only a small area of true chorion remains and the allantois is enclosed in the fold of the yolk sac membrane. In Tammar Wallabies the allantois never reaches the chorion and as gestation proceeds it accumulates urea in the allantoic fluid, presumably via the patent Wolffian ducts draining the mesonephros (Renfree 1973). A similar arrangement of foetal membranes is described for a variety of macropodids and phalangerids (Sharman 1961b; Hughes 1974; Tyndale-Biscoe & Renfree 1987). The arrangement of embryonic membranes is similar in most marsupials, although there may be considerable variation on this general pattern.
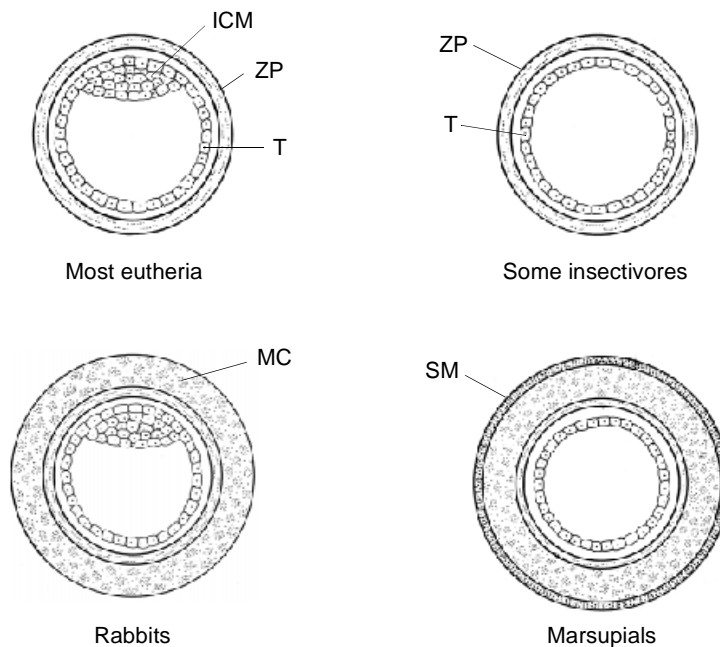

Figure 17.18 Cross-sectional views of mammalian blastocysts from the uterus prior to implantation showing comparative cellular organisation and external investments. ICM = inner cell mass; MC = mucoid coat; SM = shell membrane; T = trophoblast; ZP = zona pellucida. (Redrawn from Renfree 1982a)   [B. Scott]

In the Koala the allantois becomes apposed to the chorion and although it is vascular in the later stages, it never develops villi (Caldwell 1884; Semon 1894b; Hughes 1984). Hughes (1974, 1984) suggested that it has limited function as a chorioallantoic placenta where it is fused with the chorion; no attachment apparently occurs in the region of the vascular trilaminar yolk sac.

The most elaborate form of allantoic placentation in marsupials is found in the Long-nosed (*Perameles nasuta*), Eastern Barred (*P. gunnii*) and Southern Brown (*Isoodon obesulus*) Bandicoots, and, where a true chorioallantoic placenta is present in addition to the yolk sac placenta (Hill 1895, 1899; Flynn 1923; Hughes & McNally 1968; Padykula & Taylor 1977). An unusual feature is that in early gestation the vascular yolk sac makes the earliest contact with the chorion, its ectoderm completely fuses with the maternal luminal epithelium and 'disappears' (Padykula & Taylor 1977). The ectoderm of the chorion and the uterine epithelium are both syncytia at the time of fusion, so that foetal

capillaries come to lie close to the exposed maternal capillaries (Tyndale-Biscoe 1973; Padykula & Taylor 1977). Bandicoot neonates are relatively well developed at birth compared with other marsupials, despite their short gestation, suggesting that this group may have the most efficient placenta of all (Tyndale-Biscoe 1973; Padykula & Taylor 1977, 1982; Taylor & Padykula 1978; Tyndale-Biscoe & Renfree 1987).

The marsupials are the only group which have developed the yolk sac as the primary and, in many, the sole organ of physiological exchange throughout pregnancy. Although the allantois has retained its excretory storage role in most species, it has, with a few exceptions, lost its respiratory functions. These respiratory functions have been taken over by the yolk sac (Fig. 17.19). Metatheria may then be grouped as to placental types based on their functional aspects (Renfree 1983; Tyndale-Biscoe & Renfree 1987): groups which have retained the allantois as a placenta and the main organ of respiratory exchange, but have a yolk sac placenta with limited vascularisation (Peramelidae); groups in which there is some retention of the allantoic placenta, but the yolk sac is well developed as the main organ of exchange (Phascolarctidae, Vombatidae);
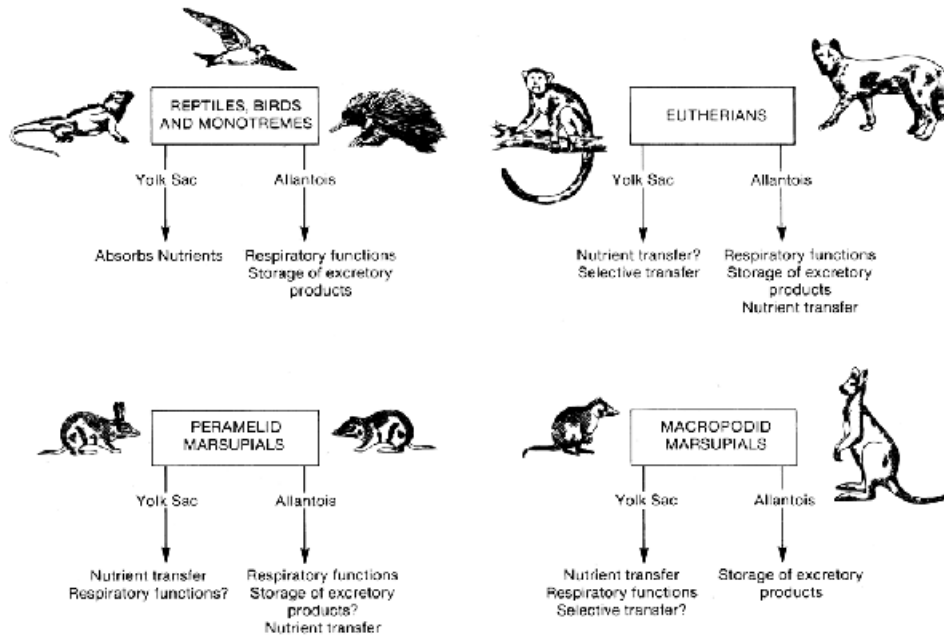

Figure 17.19 Comparison of the main types of vertebrate placental functions, emphasising the relative roles of the choriovitelline (yolk sac) placenta and the chorio-allantoic (allantoic) placenta. (Redrawn from Renfree 1977)

groups in which there is a complete loss of the allantois as the placental attachment, but in which it remains as a small, intact, vascular sac and probably functions only as an excretory store. The yolk sac is well developed and vascularised and is the only connection between mother and fetus (Macropodidae, Phalangeridae, Didelphidae).

The marsupial placenta, like that of the eutherian mammals, though variable in structure and function, is undeniably a placenta and none the less so because the attachment is more often made by the yolk sac than the allantoic membrane. Unlike the eutherian structure, the marsupial choriovitelline placenta fulfils all the nutritive and respiratory requirements of the fetus (Fig. 17.19). Although the period of placental attachment in marsupials is brief, it is of considerable importance. Likewise, in the few studies so far completed on macropodids, the marsupial placenta does have endocrine functions though these are more subtly expressed than in most eutherian mammals (see Chapter 29 this volume).

Sex differentiation

Gonads and genital ducts. Like those of other mammals, the gonads and genital ducts of marsupials are formed from three components: primordial germ cells, the coelomic epithelium that covers the genital ridge and mesodermal tissue derived from the mesonephros. In Long-nosed Bandicoots, and Northern and Southern Brown Bandicoots, which all have a gestation period of 12 days, primordial germ cells are apparent in day 8 embryos, but are found in the endoderm and mesoderm of the yolk sac and hind gut of 9.5 day embryos and in the dorsal mesentery and dorsal region of the gonadal anlagen one day before birth (Ullman 1981a). The peak of their migration occurs during the perinatal period. A similar sequence is described for Tammar Wallabies by Alcorn (1975) and Alcorn & Robinson (1983). The peak of migration occurs at about day 22 of the 27 day gestation. Likewise, primordial germ cells occur in the genital ridge of a 13 mm fetus of Common Brushtail Possums (about three days before birth) (Fraser 1919), in the neonatal Virginia Opossum (McCrady 1938; Morgan 1943) and in neonatal *Dasyurus viverrinus* (Ullmann 1984).

The gonads are at the indifferent stage at birth but differentiation occurs within a few days and, as in Eutheria the testis is recognisable before the ovary. In at least two species, the Tammar Wallaby and the Virginia Opossum, the scrotum, pouch and mammary anlagen are histologically distinct at birth (McCrady 1938; Burns 1939; Alcorn 1975; Renfree, Shaw & Short 1987). Histologically, the differentiation of the testis becomes apparent on day 2 or 3 after birth in Virginia Opossums (McCrady 1938; Burns 1939), *Perameles*, *Isoodon* (Ullmann 1981b) and Eastern Quolls (Ullmann 1984) and between day 3 and 7 in Tammar Wallabies (Alcorn 1975). In all marsupial species so far studied, the ovary can be recognised a few days later than the testis.

Urogenital system. The urogenital system, like the gonad, develops from the indifferent stage at birth to the distinctive male and female structures during the course of pouch life. The best studied species in this respect are Virginia Opossums (Baxter 1935; McCrady 1938; Burns 1939; Chase 1939; Moore 1939; Rubin 1944) and Tammar Wallabies (Alcorn 1975; Renfree *et al.* 1987) with less complete studies on other species such as Red Kangaroos (Lister & Fletcher 1881) and Common Brushtail Possums (Buchanan & Fraser 1918).

The mesonephric or Wolffian duct is patent and functions as the main urinary duct conveying urine from the mesonephros to the urogenital sinus or proctodaeum until about day 14 after birth (Tyndale- Biscoe & Renfree 1987). Running parallel and lateral to it is the Müllerian duct, which opens to the coelom near the genital ridge. At day 10 it has made connection posteriorly to the urogenital sinus near that of the Wolffian duct. The urogenital sinus opens by the genital tubercle within a common cloacal chamber. As the metanephric kidney differentiates and becomes functional (Krause, Cutts & Leeson 1979) the ureter begins to migrate ventrally to the neck of the urinary bladder. In so doing it passes medial to the connection of the Wolffian and Müllerian ducts with the urogenital sinus. In eutherians, the ureters migrate laterally to the genital ducts. The particular course of this migration has profound implications for the future development of the genital tract, particularly of the female, because the mesial position of the ureters prevents the mid-line fusion of the Müllerian ducts to form a single vagina, as occurs in eutherians (Tyndale-Biscoe & Renfree 1987). By contrast to the latter, where the Wolffian ducts (transformed to the vasa deferentia and carried with the testes into the scrotum), must loop around the ureters, in marsupials they connect directly with the urogenital tract (Tyndale-Biscoe 1973).

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