



**FAUNA**  
*of*  
**AUSTRALIA**



**16. ORNITHORHYNCHIDAE**

**T. R. GRANT**

16. ORNITHORHYNCHIDAE

## DEFINITION AND GENERAL DESCRIPTION

*Ornithorhynchus anatinus*, the Platypus, is the only extant representative of the Ornithorhynchidae, a family which has occupied the Australian mainland for at least 15 million years (Woodburne & Tedford 1975; Archer, Plane & Pledge 1978). It is a small amphibious mammal, which possesses a characteristic pliable duck-like bill and has strongly webbed forefeet. Like its living relatives, the echidnas (*Tachyglossus aculeatus* and *Zaglossus bruijnii*), the Platypus is oviparous.

## HISTORY OF DISCOVERY

The first specimen of *Ornithorhynchus anatinus* (a dried skin) reached Britain in 1798. In spite of some initial consternation over its authenticity, the animal was described by George Shaw in 1799 and named *Platypus anatinus*. It was redescribed independently as *O. paradoxus* in 1800, but later, following the rules of priority of nomenclature, became *O. anatinus* (Shaw) (*vide* Iredale & Troughton 1934). It was not until 1884 that it was finally concluded that *O. anatinus* is oviparous (Caldwell 1884b).

## MORPHOLOGY AND PHYSIOLOGY

### External Characteristics

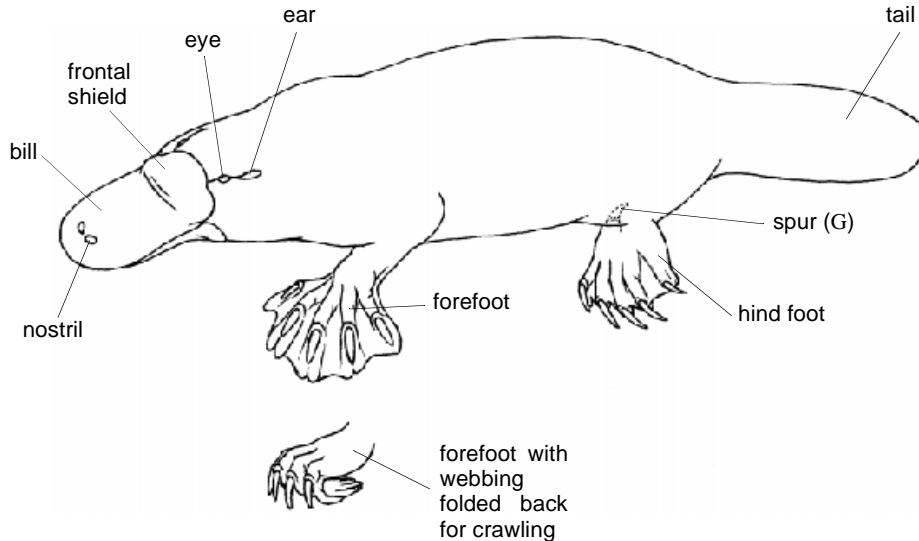
The Platypus is quite a small animal, although there is considerable size variation between populations in various parts of eastern Australia (Carrick 1983; Grant & Temple-Smith 1983). There is also a notable size difference between the sexes. Males average 500 mm (range 450–600 mm) in total length and weigh 1700 g (1000–2400 g), while females are 430 mm (390–550 mm) and 900 g (700–1600 g), respectively.

Fine, dense fur covers the body except for the bill, the complete manus, much of the pes and the underside of the tail. The dorsal surface of the tail has fur, but it is much coarser in texture and sparser than that on the rest of the body. The bill consists of soft skin applied over the elongated muzzle and lower jaw. The nostrils are situated on the dorsal surface just back from the tip. Frontal shields of skin are found at the base on both dorsal and ventral surfaces of the bill and posterior to the dorsal shield there is a groove which houses the eyes and ears. This groove is closed when the animal dives. The tail is broad, flat and is the main storage area of body fat (Hulbert & Grant 1983a). Both the manus and pes are pentadactyl. Only the former is webbed significantly; the web extends past the strong claws on the ends of the digits. The forefeet are used in swimming and their webbing is folded back to expose the claws when walking and digging. The hind feet have sharp claws which are utilised in walking and as anchors during burrowing. During swimming, the rear feet are employed only to change direction (Griffiths 1978; Grant 1984; Fig. 16.1).

The male of the species has a keratinous spur on the inside of each rear limb. These spurs are hollow and are attached by ducts to venom glands in the upper thigh regions (Temple-Smith 1973; Griffiths 1978).

### Body Wall

The skin is attached to a thick muscle layer, the panniculus carnosus. There is no distinct layer of subcutaneous fat as in *Tachyglossus*, the echidnas (Griffiths 1978). The fur is short and very dense, with the flattened blades of the guard



**Figure 16.1** The physical characteristics of the Platypus showing the most important features of its external anatomy. (After Grant 1984; © ABRS)  
[D. Kirshner]

hairs protruding above the finely kinked underfur. The structure of the pelage serves to retain air, even when the animal is in water, and contributes to the high thermal insulation of the animal (Grant & Dawson 1978b; Fig. 16.2).

### Skeletal System

The skin of the bill is supported by the elongated maxillae and premaxillae and the shorter dentaries of the lower jaw. The young lose their teeth before, or just after, they emerge from the breeding burrow. These are replaced by heavily keratinised pads in the adult. Nestlings have three teeth in each of the maxillae (one premolar and two molars) and dentaries (three molars) (Green 1937).

The Platypus has seven cervical vertebrae (Fig. 16.3), the usual number for all mammals. The ribs on these, however, and the retention of procoracoid and interclavicle bones in the pectoral girdle (Fig. 16.4) represent reptilian features of the skeleton. The pubic bones in the pelvic girdle, as in marsupials, bear epipubic bones in both sexes. The mosaic of reptilian and mammalian features seen in the developing chondrocranium was discussed by Griffiths (1978), including the development of an egg tooth in the hatchling (Green 1930).

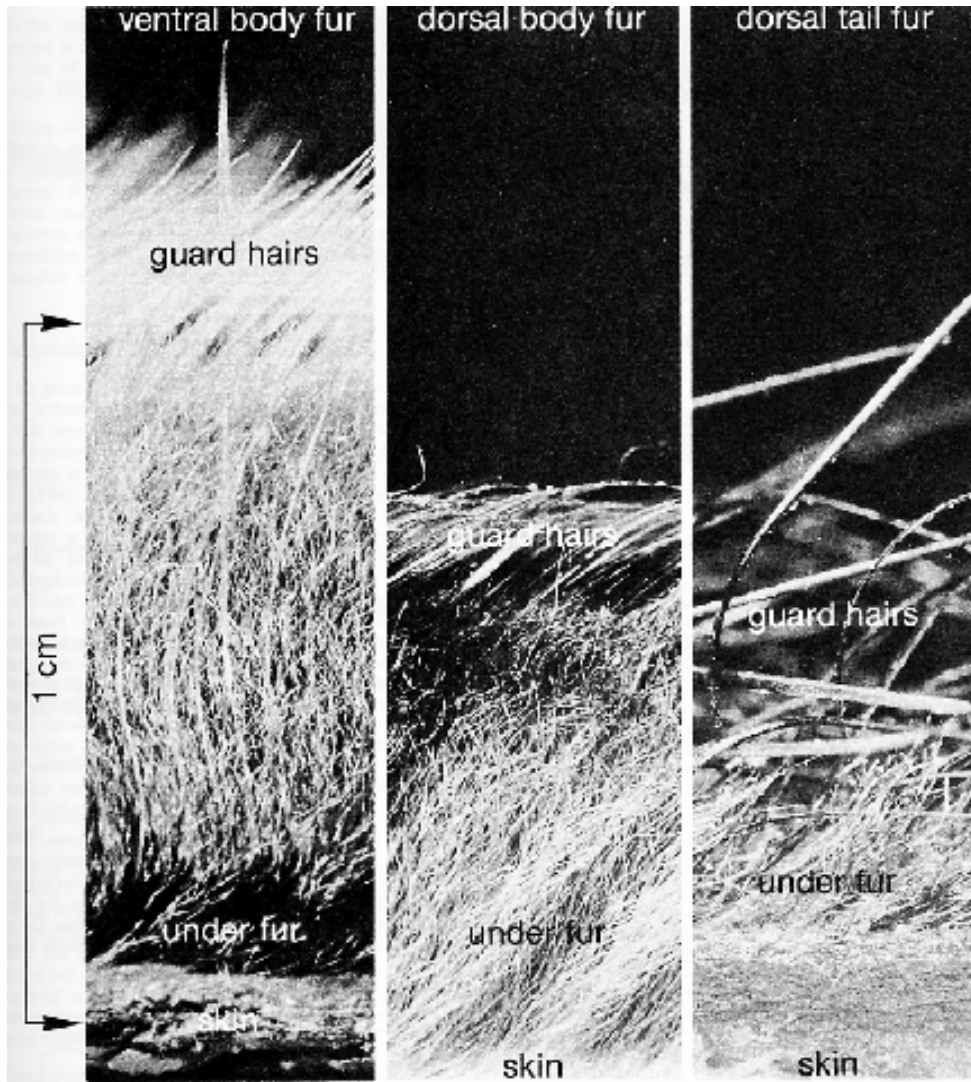
### Locomotion

On land, the Platypus carries its body close to the surface of the substratum, much less elevated than do the two species of Echidnas. At low speeds the ventral surface of the body is in contact with the substratum, but is lifted free during more rapid movement. Limb movement is close to a diagonal pattern, although the synchrony between limbs on either side of the body is not perfect (Pridmore 1978).

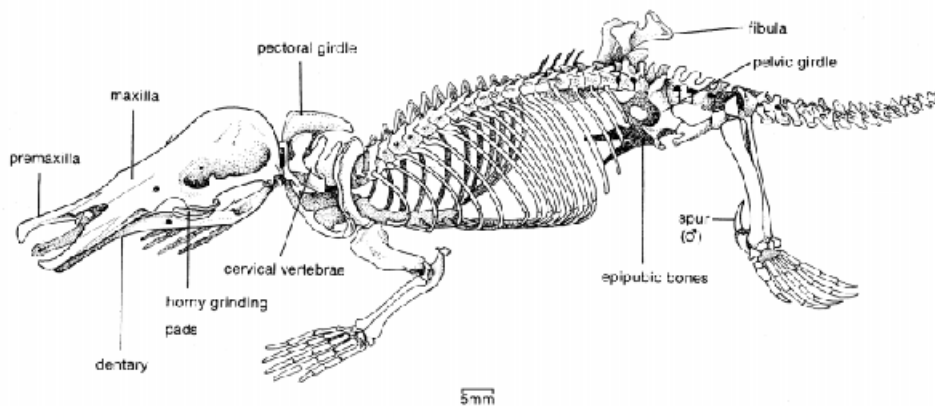
The Platypus swims by using alternate movements of its webbed forelimbs. During the back stroke, the webs are extended past the ends of the digits to present a wide surface to the water in this propulsive stroke. On return, the webs fold back to the palms where they are also held while walking and digging.

Howell (1937) indicated that, as in locomotion in the Echidna, a strong rotational movement by the broad humerus is involved in swimming. Pridmore (1978) analysed the locomotion of the Platypus and concluded that it uses

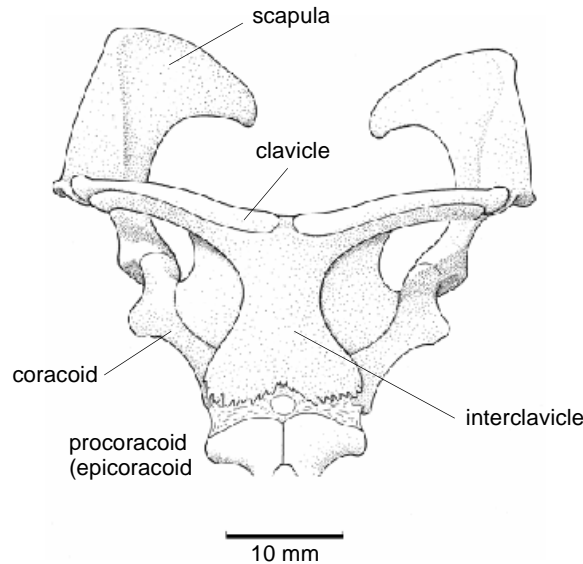




**Figure 16.2** The structure of the fur of the Platypus, showing the large flattened guard hairs overlying the dense underfur on ventral and dorsal surfaces of the body and tail. (After Grant 1984)



**Figure 16.3** The complete skeleton of the Platypus, with distinctive features labelled. (After Grant 1984; © ABRS) [S. Weidland]



**Figure 16.4** Ventral view of the reptile-like pectoral girdle of the Platypus. (After Grant 1984; © ABRS) [G. Milledge]

alternate rotational thrusts of the forelimbs in both swimming and burrowing. He further suggested that it probably evolved into its present amphibious capability via a predominantly fossorial ancestral form. Apparently, both the Echidna and the Platypus show numerous skeletal and muscular similarities in the pectoral girdles and forelimbs to the fossorial talpid moles, which also are rotational thrust burrowers. Pridmore (1985) suggested that the limb orientation in the monotremes shows modifications of a generalised therian pattern.

### Feeding and Digestive System

As mentioned above, the teeth are replaced by keratinous grinding pads in the adult. Food material, which consists mainly of benthic invertebrate species (Faragher, Grant & Carrick 1979; Grant 1982), is stored in the cheek pouches which lie adjacent to these pads. Serrations in the skin of the lower jaw are thought to be involved in sorting the masticated food particles.

The digestive tract is very simple and relatively short, 1400 mm long in a female of 440 mm (Harrop & Hume 1980). The stomach is small and thin-walled, has no gastric glands and, therefore, no peptic digestion, although Brunner's glands are present (Krause 1971). There are no villi in the short small intestine, but there are numerous surface folds. Groups of intestinal glands drain into common ducts which empty into the lumen between these folds (Krause 1975). The large intestine is also short. The rectum is of greater diameter than the rest of the tract. There is also a small caecum (Hill & Rewell 1954).

Nothing is known of the digestive processes in the species, although its diet would suggest high proteolytic activity in the secretions of both the pancreas and the intestinal wall (Harrop & Hume 1980). The food material is so finely ground once it enters the digestive tract that analysis of fragments in the cheek pouches is the only method of food recognition which has been used successfully to date (Faragher *et al.* 1979; Grant 1982).

### Circulatory System

In its gross anatomy, the circulatory system of the Platypus exhibits the typically mammalian pattern of a closed double circulation, where the systemic arch is derived during development from the left side of the fourth gill arch. This

anatomy was described in detail by Hyrtl (1853) and Hochstetter (1896). Schultz (1967) described the vascularisation of the stomach and the alimentary system and Dowd (1969b) presented a detailed study of the heart, its coronary vessels and its conducting system in both the Platypus and the Echidna. Apart from the presence of a coronary vein not found in other mammals and the indistinct sinus node, the heart of the Platypus appears to be typically mammalian in its anatomy.

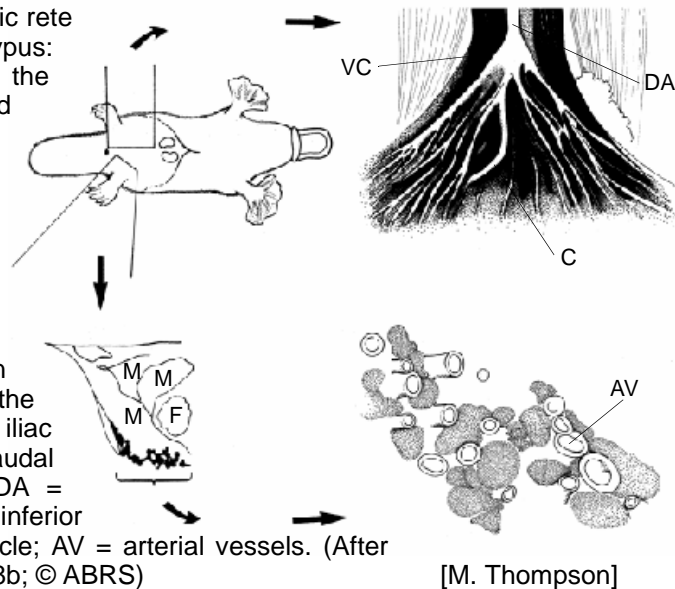
Hochstetter (1896) and Hyrtl (1853) noted the presence of a complex of venous and arterial vessels in the pelvic area with small parallel veins and arteries supplying the muscles of the rear limbs and tail. No such complex was found in the axilla, but vessels in the manus were reasonably large with much smaller ones in the extensions of the web. In both areas of the forelimb, veins (venae comitantes) tend to parallel arteries.

Grant & Dawson (1978b) confirmed these findings and suggest that both the complex rete system (Barnett, Harrison & Tomlinson 1958) arising from the short iliac arteries (Fig. 16.5) and the venae comitantes of the forelimb may serve to restrict heat loss from the unfurred extremities of the animal. The underside of the tail, the forefeet and the hind feet constitute 25.7% of the total surface area of the body. Measurements of low skin temperatures on these extremities at cold ambient temperatures substantiated this suggestion (Grant & Dawson 1978b).

**Figure 16.5** The pelvic rete system of the Platypus:

(a) ramifications of the dorsal aorta and inferior vena cava in the pelvic region of the Platypus; (b) venous vessels paralleling arterial on the surface of muscles of the thigh region.

Transverse section cut slightly distal to the branching of the iliac arteries. C = caudal artery; F = femur; DA = dorsal aorta; VC = inferior vena cava; M = muscle; AV = arterial vessels. (After Grant & Dawson 1978b; © ABRs)



Vascularisation of the bill is poorly documented. However, large venous vessels are present along its margins (Bohringer 1981) and these have been used to obtain blood samples from the species (Whittington & Grant 1983, 1984).

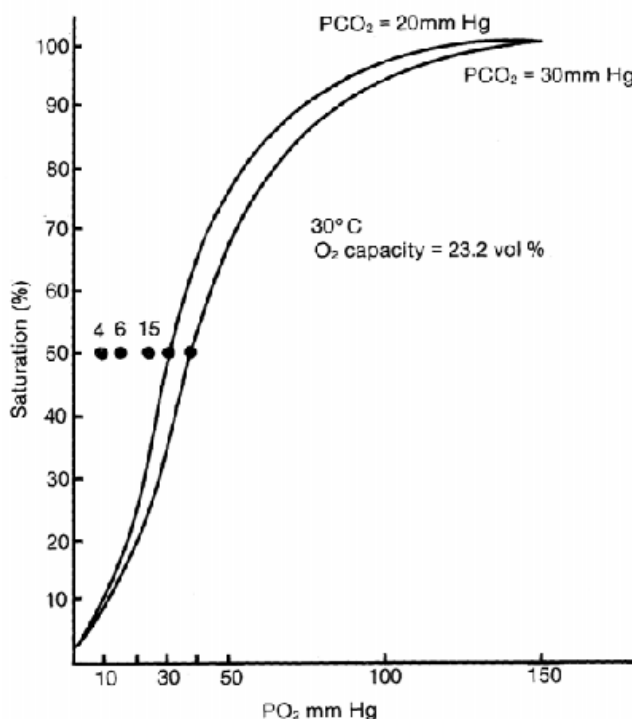
Like those of other mammals, the red blood cells of the Platypus are non-nucleate and biconcave. The platelets are also typically mammalian (Briggs 1936; Canfield & Whittington 1983). Unusual features of the leukocytes of the species, however, include the consistent presence of Döhle bodies in the segmented neutrophils and non-segmented nuclei in the eosinophils and basophils (Canfield & Whittington 1983). The species has a high haemoglobin level ( $175 \pm 4.0$  g/L) and haematocrit ( $52 \pm 1.0\%$ ) (Johansen, Lenfant & Grigg 1966; Parer & Metcalfe 1967c; Whittington & Grant 1983, 1984). These authors also found a low mean corpuscular volume ( $54 \pm 1.5 \mu\text{m}^3$ ) and a high

mean corpuscular haemoglobin concentration ( $353 \pm 6.0$  g/L), and reported a variety of white cell and blood biochemistry parameters. Similar haematological values were reported by Isaacks *et al.* (1984) in Tasmanian specimens. These authors also recorded extremely low levels of ATP in red blood cells of both the Platypus and the Echidna (0.06 and 0.03  $\mu\text{mol/ml}$ , respectively). Such trace amounts of ATP appear still sufficient to maintain active cation transport across the red cell membranes in the two species (Kim *et al.* 1984).

### Respiration

The lungs of the Platypus consist of two lobes on the right side and one on the left. There is a well-developed diaphragm at the base of the rib cage (Home 1802a).

Corresponding to its haematological characteristics, the blood of the Platypus has been found to have a high oxygen carrying capacity (about 23 ml  $\text{O}_2/100$  ml blood) (Johansen *et al.* 1966; Parer & Metcalfe 1967c). Oxygen dissociation curves for blood (Johansen *et al.* 1966) are shown in Fig. 16.6. These workers found a marked Bohr effect and bradycardia in response to forced diving which they related, along with the haematological values, to the diving physiology of the species. The Platypus does not dive for long periods or to great depths, usually spending less than 2 minutes below the water surface at one time during its foraging activities. Adult animals spend as much as 50% of their day in the burrow (Grant 1983a). Nestlings are confined to the breeding burrows for between 3–4 months (Grant, Griffiths & Leckie 1983), so it is possible that the physiological mechanisms observed by Johansen *et al.* (1966) are as much related to coping with hypoxia and hypercapnia within the burrow as to diving. The rapid reduction in the oxygen content of the blood and increased  $\text{CO}_2$  content, followed by a dramatic recovery over two minutes after a forced dive in their experimental animals, does fit well, however, with the normal pattern of diving observed in free-living animals.

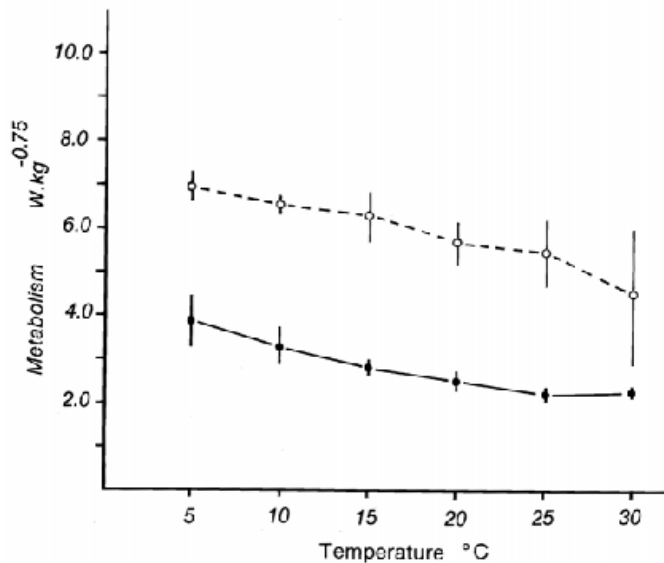


**Figure 16.6** Oxygen dissociation curves of Platypus blood. Additional values of  $P_{50}$  at 4, 6 and 15 mm Hg  $\text{PCO}_2$  are shown, indicating the Bohr Effect. (From Johansen *et al.* 1966)



The Platypus can adequately regulate its body temperature in air between temperatures of 0–30°C (Martin 1902; Smyth 1973; Grant & Dawson 1978a, 1978b), but does not cope well with air temperatures above 30°C (Robinson 1954; Grant & Dawson 1978b). It is also a competent homeotherm in water (Grant & Dawson 1978, 1978b; Grant 1983a).

The normal body temperature of the Platypus is  $32.0 \pm 0.4^\circ\text{C}$  (Grant & Dawson 1978a). This low, but constant, temperature is maintained by the elevation of metabolic rate seen in all endothermic species. The standard metabolic rate at the thermoneutral temperature of  $25^\circ\text{C}$  in air is  $2.2 \text{ W kg}^{-0.75}$  and can be elevated to 1.8 times this at an air temperature of  $5^\circ\text{C}$  and to 3.2 times in water of the same temperature (Grant & Dawson 1978b; Dawson, Grant & Fanning 1979) (Fig. 16.7). Radiotelemetric studies on free-ranging animals in the wild have shown that body temperatures are maintained close to  $32^\circ\text{C}$  during foraging periods of many hours in water as cold as  $0^\circ\text{C}$  (Grant 1983a).



**Figure 16.7**  
Metabolism of the Platypus in air and water of different temperatures. Means  $\pm$  S.E. are shown. (From Grant & Dawson 1978b)

Homeothermy is achieved not only by elevation of metabolic rate, but also by virtue of the high thermal insulation which results from both reduced tissue conductance at low ambient temperatures and the high insulative value of the fur and its associated layer of air ( $0.33 \text{ W}^{-1} \text{ m}^2 \text{ }^\circ\text{C}$  in air). Although the fur loses 60–70% of its insulative value in water and tissue insulation becomes more important, the fur of the Platypus still contributes more significantly to total body insulation in water than the fur of many other amphibious mammals. High tissue insulation presumably is achieved by the restriction of heat loss to the environment through the unfurred extremities. Skin temperatures at low ambient air and water temperatures are kept at only  $1\text{--}2^\circ\text{C}$  above ambient. Occupation of a burrow, which buffers environmental temperature changes in both summer and winter conditions, also contributes to thermoregulation in the species (Grant & Dawson 1978b; Grant 1983a).

There have been various reports of hibernation or torpor based on captive specimens (Eadie 1935; Fleay 1944, 1980). This has not been observed in the wild, but it is possible that the species exhibits torpor in response to cold and food shortage as does *Tachyglossus aculeatus* (Augee & Ealey 1968). Studies on the activities of the enzymes lactate and malate dehydrogenase from the Platypus and on oxygen consumption of various tissues *in vitro* over a range of temperatures have produced equivocal results in trying to relate these to the

lability of body temperature in either the Platypus or the Echidna (Aleksiuk & Baldwin 1973; Baldwin & Aleksiuk 1973). In both studies, the responses obtained appear to be most like those expected for a homeothermic species than for a heterotherm.

### Excretion

There is no published information on renal structure or function in the Platypus. Not unexpectedly for a species which obtains its food entirely in water, water turnover in free-living animals is very high (480 ml/day) (Hulbert & Grant 1983a).

### Sense Organs and the Nervous System

Hines (1929) gives a detailed description of the brain of the Platypus. This and later observations were summarised by Griffiths (1978). The brain is relatively large and is essentially mammalian in its organisation. The neocortex is very large in relation to the pyriform and hippocampal cortices. Unlike that of the Echidna, the brain of the Platypus is not highly fissured, but is lissencephalic. There is no corpus callosum joining the two hemispheres, though there is communication between the two halves of the telencephalon through the anterior and hippocampal commissures.

The olfactory bulb is well developed, but, as in the Echidna, it lacks the well-defined layer of mitral cells found in all other mammals. Nothing is known of olfaction in the animal and the physiological importance of the absence of these cells is open to question (Griffiths 1978). Hines (1929) found the olfactory pathways in the brain to be similar to those in other mammals. As the nostrils are closed by a valve in the bill during diving, olfaction probably is not important in foraging behaviour. Griffiths (1978) suggested, however, that olfaction may be important in courtship and in the reflex induction of milk ejection in lactating females. It may be important in other social behaviour patterns. Both sexes have well-developed sternal scent glands. Burrell (1927) noted marking of burrows by males with a 'foxy odour'. Strahan & Thomas (1975) reported that a captive male deposited mucous-like secretions over underwater objects, but noted that the female did not appear to react to these secretions. This latter behaviour is, therefore, difficult to interpret.

Jacobson's Organs are present, opening into the buccal cavity, and are probably associated with smelling food in the mouth (Griffiths 1978).

The vallate foliate papilla complex, associated with taste in mammals, is found in both the Echidna and the Platypus in grooves on either side of the dorsal surface of the tongue (Brightman 1976).

The eye of the Platypus is supported by a cartilaginous cup, a structure not found in any metatherian or eutherian species. There is a nictitating membrane, lachrymal and Harderian glands are present and both lids have tarsal plates. The pupil is round, with a sphincter of smooth muscle, the choroid is unusually thick and deeply pigmented and the retina has rods and double cones with colourless oil droplets. Although the internal structure of the eye is mammalian, the scleral cartilage, the double cones and the oil droplets are sauropsidan characters (Newell 1954). The eye is small (6.0 mm diameter), spherical, and has a flat lens which would appear to give it little accommodation ability, but to adapt it more to vision in water than in air (Walls 1942). Griffiths (1978) indicated that this is of little importance, as the Platypus closes its eyes when underwater. Green (1984) photographed two captive specimens momentarily opening their eyes while diving. For a species which forages for its food mainly in turbid waters and mainly at night, a reliance on visual sensory input would seem a paradox.

Moreover, Pridmore (personal communication) found that captive animals could navigate and feed with their eyes covered. Although it has poor capacities for accommodation, the eye is extremely sensitive to movements while the animal is on land or on the surface of the water. Patently, more investigation on the nature of vision is required.

Primary optic pathways have been investigated in the central nervous system (Campbell & Hayhow 1972). There are few fibres in the optic chiasma which pass to ipsilateral sides of the brain. Positioning of the eyes in the grooves (which also house the ear openings) on each side of the head and posterior to the extensions of the frontal shield suggests that the species is unlikely to possess stereoscopic vision.

Gates *et al.* (1974) studied cochlear microphonic potentials of the ear of the Platypus in response to sounds of differing frequencies. The middle ear bones consist of the malleus, incus and stapes, as in other mammals, but the articulation between the malleus and incus is unusual. The stapes is columelliform as it is in the Echidna, marsupials and pangolins. Although the cochlea is not coiled and resembles that of Mesozoic mammals, its internal structure is mammalian, as is the organisation of its organ of Corti.

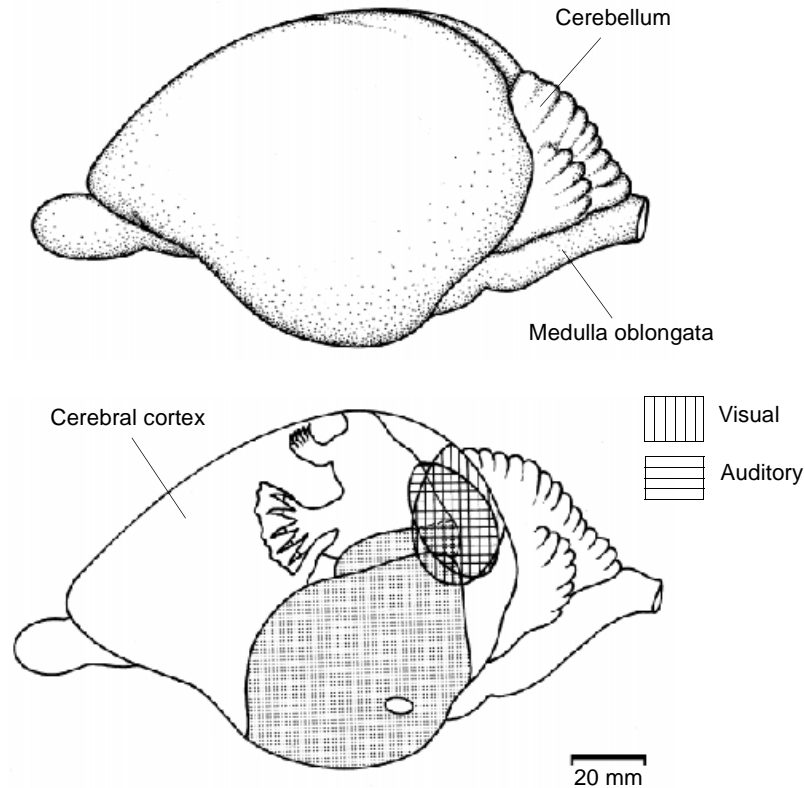
Although the cochlea was found to respond to a reasonably wide range of frequencies of sound, it was less sensitive than the cochlea of most other mammals, including the Echidna. This lack of sensitivity compared with other mammals was attributed to differences in structure. The slight reduction in sensitivity below that of the Echidna is thought to be due to dissimilarities in the middle ears of the two monotremes. The conclusion, however, is that audition in both of these animals is more similar to that found in marsupials and eutherians than it is to reptiles (Griffiths 1978).

For an animal which closes its ears, eyes and nostrils when diving, underwater navigation and location of food would seem to present a problem. Home (1802a) noted the massive innervation of the bill, while Poulton (1885) recorded the occurrence of numerous peripheral nerve terminals within the skin of the muzzle. Until neurophysiological measurements were made by Bohringer & Rowe (1977), little of the nature of the tactile sense of this organ was established.

These workers found a large area of representation of nerves from the numerous nerve terminals, or rod organs, in the sensory cortex (Fig. 16.8). This area was much larger than those which represented either the visual or auditory inputs. Within the large area of bill representation, individual neurones were found to have very restricted receptive fields. Bohringer (1981) further described the rod organs associated with the many small pits in the bill (distinct from the larger ones associated with sweat glands) and suggests they function to permit tactile reception of a very sensitive nature, but still allow physical protection of the muzzle by the keratinised epidermis.

The sequential stimulation of rod organs in a specific order may permit the Platypus to localise its position or the position of its food by the evaluation of both static and moving components of tactile stimuli. Andres & von Doring (1984) reconstructed the fine detail of the rod organs and suggest that their innervation makes them a possible three-dimensional detection system. These workers also indicate the possibility of the transmission of water movement direction and pressure through the secretion films and tonofibrils to the nerves associated with the gland ducts in the bill. How the Platypus manages to move about underwater, avoiding objects and finding its prey without actually having to touch them with its bill, is not completely clear.

In a recent study, Scheich *et al.* (1986) found that captives respond to small electrical fields in water. Individuals are attracted more frequently to submerged miniature 1.5 V batteries and to fields generated between two carbon electrodes



**Figure 16.8** Organisation of the sensory cortex: (a) brain of the Platypus showing the lissencephalic nature of the cortex; (b) the brain has a Platypus figurine (stippled) drawn in proportion to the amount of representation of each area in the cortex. Areas receiving sensory input from the eyes and ears are also shown. (After Bohringer & Rowe 1977; Grant 1984; © ABRS) [M. Thompson]

than to spent batteries or when fields were turned off. Animals also respond with reflex head and tail movements to fields in water between aluminium plates placed 3 m apart, at threshold values from between  $50 \mu\text{V}/\text{cm}$  and  $500 \mu\text{V}/\text{cm}$ . These authors also record cortical evoked potentials from electrical stimulus to wet cotton on the bill and suggested electroreception mediated via the trigeminal system, with representation in the cortex next to the trigeminal map of bill mechanoreceptors mapped by Bohringer & Rowe (1977). These latter authors found that motor areas of the cortex overlapped sensory areas.

### Endocrine and Exocrine Systems

According to Griffiths (1978), citing the work of Hanstrom & Wingstrand (1951), the anatomy of the pituitary is like that of a reptile and very like that of the Echidna. The neurohypophyseal hormones of the Platypus appear to be similar to those of the Echidna and to those of most placental mammals. Chauvet *et al.* (1985) identified two peptides from the posterior pituitary of the Platypus. One is identical to arginine vasopressin in its amino acid composition and chromatographic retention time. This pressor peptide is approximately four times more abundant than the oxytocic peptide found. The amino acid composition of this latter peptide has not been determined.

The adrenal glands lie in contact with the kidneys close to the exit of the ureters and are about  $18 \times 8$  mm in size. In these glands, the chromaffin tissue is located in the caudal region and the cortical tissue in the anterior part of the gland. There is, however, no distinct boundary between the



tissues. There are three recognisable types of cortical cells, but these apparently are not segregated into concentric zones as in the adrenals of eutherian and marsupial mammals (Griffiths 1978; McDonald 1978). Unlike the Echidna, which has small adrenals in relation to its body size, those of the Platypus are in the range of eutherian mammals ( $257 \pm 41 \text{ mg kg}^{-1}$ ; Weiss 1973; McDonald 1978).

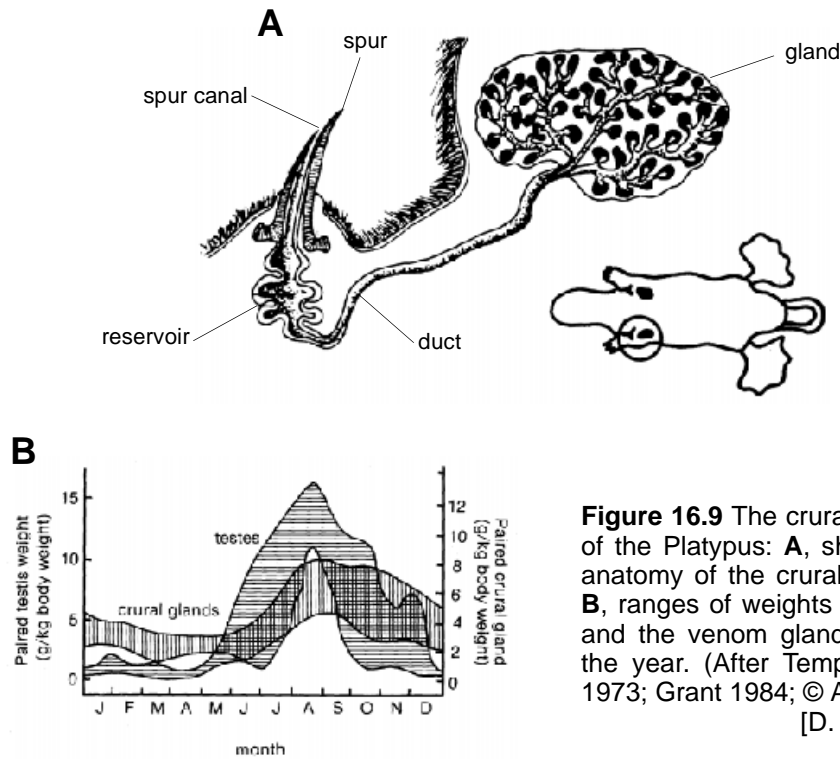
Weiss (1973) identified and measured four adrenal corticosteroids in peripheral blood of the Platypus. These are cortisone ( $8.2 \mu\text{g}/100 \text{ ml plasma}$ ), cortisol ( $5.4 \mu\text{g}/100 \text{ ml}$ ) and combined corticosterone and 11-dehydro-corticosterone ( $1.8 \mu\text{g}/100 \text{ ml}$ ). The total corticosteroid level is within the range of values for eutherian mammals, although the major glucocorticoid in Platypus blood is cortisone, which normally occurs in negligible concentrations in the blood of other mammals (McDonald 1978). The enzyme systems for the biosynthesis of corticosteroids in both the Echidna and the Platypus appear to be similar to those found in eutherian mammals (Weiss 1973; McDonald 1978). Higher levels and secretion rates of these hormones compared to the Echidna have been attributed to a more significant role of the adrenal glands in the regulation of metabolism in the Platypus (McDonald 1978). Although there is considerable variability in the data, McColl (1983) found increases in both total adrenal weight and in the ratios of adrenal weight to body weight in 20 specimens which had died under captive conditions.

Serum thyroxine (T4) and triiodothyronine (T3) levels were measured in the blood of wild-caught *Ornithorhynchus* (Hulbert & Grant 1983b). There is little seasonal difference in the levels of either hormone. Males have significantly higher levels of T3 than females. Juveniles show levels above adults of both T3 and T4. The measured 37–136 nmol/L for T4 and 0.3–1.7 nmol/L for T3 were higher than those found in marsupials and Echidnas and may be associated with the relatively high metabolic and growth rates in the Platypus.

Six kinds of endocrine cells have been identified in the proximal small intestine of the Platypus and five types of neuropeptide have been detected in the intramural nerve elements of this region. The functional significance of these endocrine cells and the neuropeptides in the species is unknown, but the smooth muscle regulatory substances may be involved with contraction and expansion of the intestinal folds, which may compensate for the absence of villi (Yamada & Krause 1983).

Both eccrine and apocrine sweat glands are found in the skin of the Platypus on all parts of the body and particularly on the margins of the frontal shield (Montagna & Ellis 1960). These glands secrete sweat at room temperature and, in response to subcutaneous injection of adrenalin, at an ambient temperature of  $5 \text{ }^\circ\text{C}$  (Augee 1976; Grant & Dawson 1978b). They are, however, ineffective in evaporative cooling of the animal at high ambient temperatures, presumably because of their position under the dense fur (Robinson 1954; Grant & Dawson 1978b). Their secretions possibly are involved in the water-repellent properties of the fur.

Male Platypuses have an alveolar, reniform venom gland located on the dorsal aspect of the upper thigh muscles of each rear limb. Size and histological changes in this gland occur during the year, paralleling changes in the testes (Fig. 16.9). Secretory products are released from the cells of a single layered secretory epithelium by eccrine and apocrine extrusion and consist mainly of proteinaceous material. The major components of the secretion are pre- and postalbumins and several larger proteins. Both the volume and components of the venom change with seasonal recrudescence and regression of the gland. The active component of the venom is not known, although it is apparently not a neurotoxin. Invenomation, especially in the breeding season, causes intense pain in humans. When the species was hunted for its pelt, gun dogs were used to



**Figure 16.9** The crural system of the Platypus: **A**, shows the anatomy of the crural system; **B**, ranges of weights of testes and the venom glands during the year. (After Temple-Smith 1973; Grant 1984; © ABRIS) [D. Fanning]

retrieve animals, stunned in the water by the close impact of a round from a heavy calibre rifle. There are recorded instances of such dogs dying from being spurred in the muzzle region (Temple-Smith 1973; Griffiths 1978).

## Reproduction

In both sexes the diploid chromosome number is 52, associated with an XY (male) and XX (female) sex chromosome mechanism. A chain multiple of ten forms at male meiosis which involves the sex chromosomes (Murtagh 1977).

The gross anatomy of the male and female reproductive systems in both *Ornithorhynchus* and *Tachyglossus* is very similar. These are described by Griffiths (1984, this Volume). In the Platypus only the left ovary is functional. The eggs (one to three; Burrell 1927) are thought to be laid onto the ventral abdomen where they are incubated at around body temperature (Griffiths 1978; Grant 1983a). As the body temperatures of both Australian monotremes are similar (Dawson *et al.* 1979), the eggs are of similar size (about 15 x 17 mm) and the developing embryo is at the 19 to 20 somite stage at laying in both species (Hughes & Carrick 1978). Incubation in the Platypus is assumed to be about 10 days, as in the Echidna (Griffiths 1978). No pouch develops and the young are not carried by the mother.

Flynn & Hill (1939) gave a detailed description of development of the eggs of both species from oogenesis to hatching. These observations, which did not distinguish between the Platypus and the Echidna, are described in detail by Griffiths (1978, this Volume). Gestation is thought to be of similar duration as in *Tachyglossus* (about 27 days; Griffiths 1978) and based on one observation by Hughes & Carrick (1978), is at least 9 days. During this time, pregnancy is thought to be maintained by the secretion of progesterone and oestradiol-17 $\beta$  from the functional equivalent of the corpus luteum, which develops from the apparently sauropsid-like ovarian follicle. Similar levels of these two hormones to those measured in pregnant eutherian mammals have been observed in the Platypus during gestation (10.4 ng/ml progesterone, 0.16 ng/ml oestradiol;

Hughes & Carrick 1978). During gestation, nutrients are supplied to the growing embryo through the mucoid coat and shell of the egg from the walls of the uterus (Griffiths 1978; Hughes & Carrick 1978).

Although reproductive activity occurs in the spring, there is a spread in breeding times within populations and in different localities. Onset of reproductive activity seems to occur earlier in the north than in the south (Burrell 1927; Temple-Smith 1973; Griffiths 1978; Grant *et al.* 1983). Growth of the uteri and ovarian follicles has been found to commence late in June, attaining maximum values in August, regressing to a minimum by December (Temple-Smith 1973). The left ovary also achieves its maximum weight in relation to body weight in August and regresses during the summer. No corresponding changes are seen in the right ovary, but some development occurs in the right uterus (Griffiths 1978).

The testes are abdominal (testicond). They undergo similar changes during the breeding season and reach their maximum weight in relation to body weight in August/September (up to 16 g/kg) before undergoing marked involution by January (about 1 g/kg) (Carrick & Hughes 1978; Griffiths 1978). The high levels of testosterone found in the testicular vein during the breeding season (400 ng/ml plasma), fall to low levels (10 ng/ml) on involution of the testes (Carrick & Hughes 1978). Similar changes occur in the size of the venom gland associated with the spur apparatus (crural system) in the male (Temple-Smith 1973) and the significance of these are discussed above (Fig. 16.9).

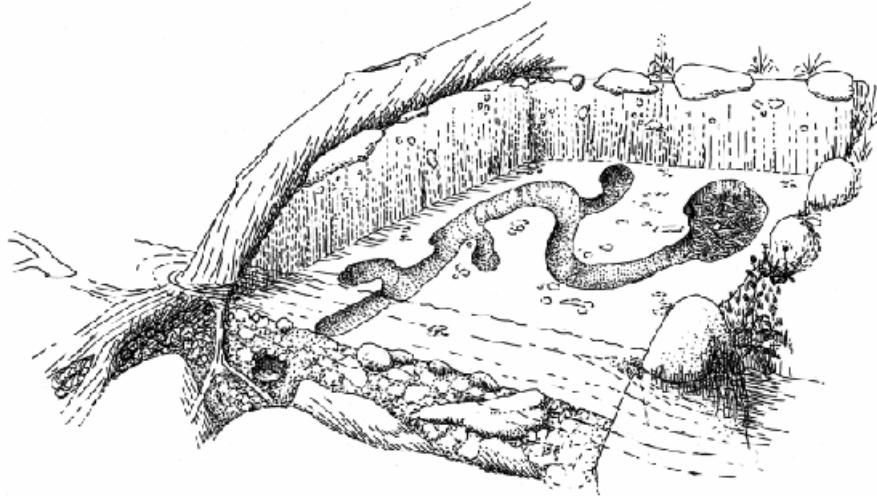
The testis is reptilian in structure (Griffiths 1984). It exhibits some distinctive features not seen in eutherians or metatherians and the epididymis associated with it is comparatively very large. These features are discussed in detail by Carrick & Hughes (1978) and Griffiths (1978). The distinctive filiform spermatozoa possess some features seen in marsupial sperm and some that occur in the sperm of sauropsids. They have, however, a number of their own characteristic features, as well as showing a close affinity with the unspecialised spermatozoa of some eutherian mammals (Carrick & Hughes 1978).

### Embryology and Development

Details of embryology from fertilisation to egg-laying, when the embryo is at the 19 to 20 somite stage of development, are described for both the Platypus and the Echidna by Griffiths (1978, this Volume), as are the details known concerning the embryology and development of the Echidna after hatching. Little is known about these in the Platypus. Because of the similarities between the neonate of marsupials and the newly-hatched monotreme and in the respective fetal membranes, the suggestion has been proposed that ancient marsupials may have been oviparous. Their present strategy, therefore, would be derived by incorporation of the incubation period into the intrauterine period (Luckett 1976; Griffiths 1978).

Apart from the specimens of Burrell (1927), the ages of which must remain speculative because of the spread of breeding within populations (Grant *et al.* 1983), little is known of the development of the young as it occurs within the confines of the breeding burrows. These burrows are long (up to 30 m) and complex structures (Fig. 16.10) which are built and apparently reworked from season to season by breeding females (Burrell 1927). In 70 nests excavated by Burrell, only five contained three eggs or young and the rest contained two (54) or one (11). Nothing is known of the survival of young from litters of different sizes.

For 3–4 months the young are suckled by their mothers in the burrows (Griffiths 1978; Grant *et al.* 1983). The female lacks teats and the young are assumed to suck milk from the fur around the areolae of the two glands. When the young emerge in late summer they are fully furred and are around 67% of adult weight



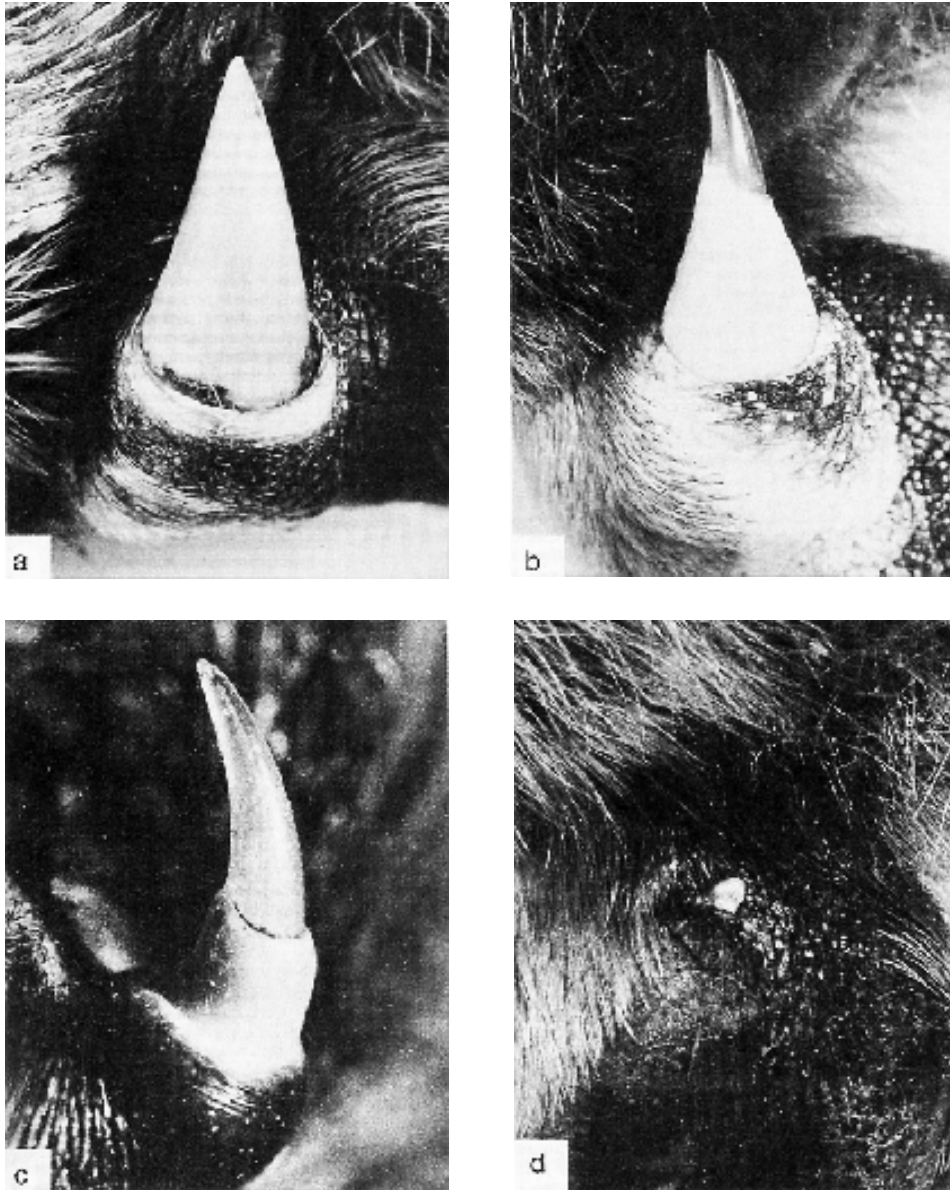
**Figure 16.10** A cut-away diagram showing the complexity of the nesting burrow of the Platypus. (After Burrell 1927; © ABRS) [G. Scott]

and 80% of the length of adults of each sex (Grant & Temple-Smith 1983). From May to July, the mammary glands are quiescent, very small (Griffiths 1978) and consist of lobules up to 25 mm filled with highly coiled duct tissue without lumina. Towards the end of July, a period of growth and differentiation results in glands with lobules of around 49 mm with distinct lumina. They are found in females in the months of October to January (Grant *et al.* 1983). These regress by January if pregnancy does not occur. If egg-laying occurs, lactating females develop expanded, branching tubules divided into a fully alveolar condition and this condition persists throughout lactation (Griffiths 1978).

The milk, like that of the Echidna, contains more total solids than that of many eutherian species with 39.1% by volume total solids: 22.2% crude lipid, 8.2% crude protein, 3.3% hexose sugar and 0.43% sialic acid. The major oligosaccharide in the milk is difucosyllactose and there is very little free lactose. There is also a high concentration of iron as in the milks of marsupials and *Tachyglossus*, all of which have very small neonates or hatchlings with a correspondingly small liver (Messer, Gadiel, Ralston & Griffiths 1983; Griffiths *et al.* 1984). Details of the lipid and carbohydrate composition of *Ornithorhynchus* milk were given by Griffiths (1978), Grant *et al.* (1983), Messer *et al.* (1983) and Griffiths *et al.* (1984). There is no evidence of change in the composition of these milk constituents over the months of lactation.

Post-hatching development of the crural system in the Platypus has been studied closely from nestling to adult stages (Temple-Smith 1973; Temple-Smith & Grant 1982). In nestlings, the spur develops within a conical sheath of dense connective tissue enclosed by a thick, keratinised epithelium. In males, the sheath grows to about 10 mm in length during the nestling period, but in the female reaches only 2.5 mm. More extensive development of the spur of the male occurs also during this period. In juvenile males, growth of the sheath and spur continues until April, about 2 months after weaning. No further changes are visible until the sheath begins to disintegrate around July, to reveal the spur by about October. Even after complete exsheathment, juvenile males can be distinguished until March by a wide epidermal collar around and some way up the spur. The female spur sheath increases to about 5 mm by July, then disintegrates to reveal a short spur which is lost in most animals by October of the first year. Remnants have been seen on one or other ankle of some animals as late as December (Fig. 16.11).





**Figure 16.11** The spur morphology of the Platypus: (a & b) growth stages of the spur of juvenile males; (c) spur of adult male; (d) rudimentary spur of a juvenile female. (After Temple-Smith 1973; Grant 1984) [Photos by P. Temple-Smith]

These changes in spur morphology have proved useful in the assessment of recruitment of young animals to populations after the breeding season (Grant 1984).

## NATURAL HISTORY

Probably because of its small size, secretive habits and often nocturnal activity, the natural history of the Platypus has not been well studied. Apart from valuable, but mainly anecdotal observations by Burrell (1927), Fleay (1944, 1980) and others as well as recent work by the author and his co-workers (Grant 1984), there exists a dearth of knowledge regarding the field biology of the Platypus. Much work on the ecology and behaviour of the species needs to be done, especially that aimed at its management and conservation in a habitat which is increasingly subject to disturbances by humans.

## Life History

If the general concept of reproductive strategies ranging along a continuum from  $r$  to  $K$  selected species (Stearns 1976) is accepted, the Platypus must be considered  $K$  selected. It is long-lived, with individuals recorded as living for up to 17 years in captivity (Carrick, Grant & Williams 1982) and females of over 11 years of age breeding in the wild (Grant & Griffiths 1984). Considerable effort is expended in the care and maintenance of the few offspring. Although there is a steady recruitment to populations each year, not all adult females breed each season and most do not breed until at least their third year of life (Grant *et al.* 1983; Grant & Griffiths 1984).

Survival of adult animals seems to be high. Grant (1984) recaptured 60% (50% of males and 65% of females) of all adults marked in the upper Shoalhaven River in New South Wales, while recapturing only 18% of marked juveniles over the same period in the same area. This latter observation may indicate juvenile dispersal, high juvenile mortality or that both factors operate in wild Platypus populations.

## Ecology

Little is known of mortality factors acting upon the Platypus in the wild. Burrell (1927) remarked that 'natural enemies of the Platypus appear to be few in number' and lists carpet snakes, goannas and possibly whistling eagles and Murray cod as predators. Little evidence is provided to support these suggestions. More recently, crocodiles, eels, water rats, foxes and even a Grey Goshawk (Richards 1986c) have been implicated in predation by isolated casual observations, but there is no evidence of regular predation on the species.

Diseases and parasites also are poorly documented, particularly with respect to their possible contribution to mortality. Whittington & McColl (1983) recorded death by aspiration of plant material, followed by *Escherichia coli* and *Aeromonas hydrophila* infection of a lactating female animal after severe localised flash flooding in an area near Wollongong in New South Wales. Fatal multiple ulceration of the skin in four specimens associated with infection by achloric algae, was reported from the Elizabeth River in Tasmania (Munday & Peel 1983). McColl & Whittington (1985) found titres of antibodies to *Leptospira interrogans* (serogroup *Hebdonadis*) in 50% of the blood samples taken from specimens in the upper Shoalhaven River. There was insufficient evidence for these workers to state whether or not infection causes disease in the species.

Parasites of *Ornithorhynchus* include: the protozoans, *Theileria ornithorhynchi*, *Trypanosoma binneyi* (Mackerras 1959) and *Eimeria* species (McColl 1983); the nematodes, *Maritrema ornithorhynchi* (Hickman 1955a), *Mehlisia ornithorhynchi* and *Moreauia mirabilis* (Mackerras 1958); the nematodes, *Capillaria* species (Munday & Peel 1983) and possibly *Tasmanema mundayi* (Durette-Desset & Cassone 1983; Mawson 1973); the fleas, *Pygiopsylla hoplia* and *P. zethi* (Dunnett & Mardon 1974); and the ticks, *Amblyomma triguttatum* and *Ixodes ornithorhynchi* (Roberts 1970). Large numbers (>100) of the latter tick, particularly small instars, occur at some times on certain individual animals, concentrated around the pelvic region and rear limbs (Temple-Smith 1973). These do not seem to noticeably affect the physical condition of animals. Whittington & Grant (1983) found no correlation between tick load and any of the measured haematological parameters.

There appears to be considerable site attachment of certain individuals in Platypus populations (Temple-Smith 1973; Grant & Carrick 1978; Griffiths 1978; Grant 1983b). Although most animals forage over a range of less than 1.5 km (Grant & Carrick 1978), movements of over 3 km have been recorded.

Animals negotiate numbers of riffle areas over these distances and even enter tributary streams (Temple-Smith 1973; Grant & Carrick 1978; Grant 1983b). Grant (1983a) radio-tracked a juvenile male which moved 3.5 km downstream from its point of capture over a period of four days. This, and the failure to recapture some marked adult animals and many juveniles in the upper Shoalhaven River, suggest the possibility of longer distance movement, especially by juveniles. Site attachment appears to be maintained by at least some individuals, even during flooding of their habitat (Grant & Carrick 1978; Griffiths 1978).

The Platypus is active throughout the night, but, particularly in summer, there is a burst of activity around dusk. High rates of capture indicate many animals begin to forage at this time. Some forage throughout the night. Others leave the water for varying periods and may feed during daylight hours, especially in winter (Grant 1983a, 1983b). On average, the Platypus spends about 50% of its day in the water and the rest of the day in burrows which are shorter and simpler in construction than the breeding burrows (Burrell 1927). During foraging, individuals may use several of these burrows (Grant 1983a).

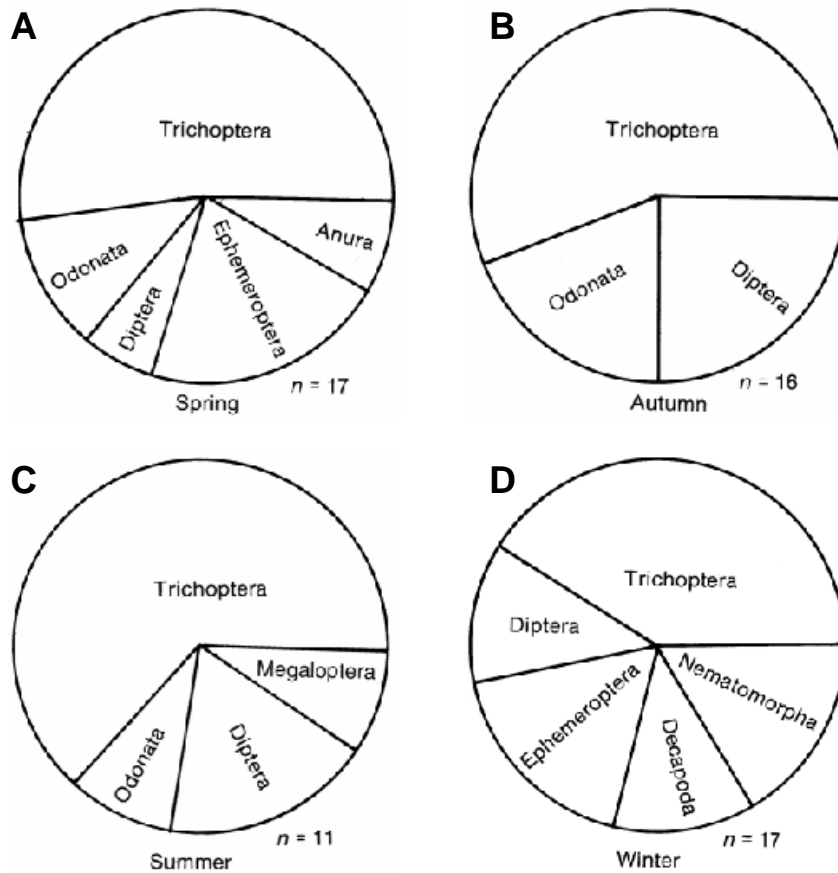
As noted previously, the food of the Platypus consists mainly of benthic invertebrates, especially insect larvae. The remains of a small frog or tadpole were found in the cheek pouch of one animal and some have been reported to take Brown Trout (*Salmo trutta*) eggs during the spawning season (Faragher *et al.* 1979; Grant 1982). Captive specimens occasionally will take the Mosquito Fish (*Gambusia affinis*) as food. Although there is some anecdotal evidence that small fish are taken in the wild (for example Nicholls 1958), no fish scales have been found in cheek pouch samples taken from five different drainage systems (Grant 1982). Seasonal changes in diet (Fig. 16.12) indicate that the species is opportunistic in utilisation of prey species (Faragher *et al.* 1979).

## Behaviour

Little is known of the behaviour of the Platypus especially in the wild. Fleay (1944, 1980) described behaviour patterns observed in captive animals, including a female carrying nesting material in its tail. Strahan & Thomas (1975) gave details of observations of courtship and a possible copulation in two animals at Taronga Zoo in Sydney. The elements of courtship included following and tail- and neck-holding by the male, with both sexes carrying out passing movements beside and under each other. Two eggs were laid by the female, but were not incubated successfully.

Males are known to interact aggressively at the start of the breeding season (Burrell 1927; Fleay 1980). During the breeding season, the crural glands enlarge in parallel with the testes (Fig. 16.9). Males may establish territories or possession of particular females at this time by fighting with their spurs (Temple-Smith 1973). Burrell (1927) presented evidence to support this hypothesis, which had been proposed by earlier naturalists, but finally accepts the notion that they were used in defence and to grip the female during copulation. Neither the observations of Strahan & Thomas (1975) nor those of Fleay (1980) supported this latter view.

Diving is normally a silent event. When disturbed, the dive is accompanied by a notable splash. Fleay (1980) suggested that this splash is a warning signal to other individuals in the area. A low growl is the most common vocalisation and is heard when an animal is disturbed in captivity or when handled in the wild (Fleay 1980; Carrick 1983). Nothing is known of vocalisations under natural conditions.



**Figure 16.12** Seasonal composition of the diet of the Platypus. (From Faragher *et al.* 1979)

Although the Platypus is usually considered to be largely a solitary species, male-male interactions, probable dispersal of young, the non-breeding of some adult females in populations and the possession of the crural system indicate that the species may exhibit quite complex social organisation.

### Economic Significance

The Platypus was protected in all States in which it occurred by the early 20th Century (for example the Native Animal Protection Act of 1906 in Queensland; the Animal and Bird Protection Act of 1907 in Tasmania and the Amendment to the Bird Protection Act of 1901 in New South Wales). Prior to this, it was hunted for its fur. Only a limited overseas market for its pelt apparently existed (Poland 1892) as it is difficult to work into garments (Burrell 1927), but there was reputedly a considerable local trade which may even have affected the status of the species in some areas (Burrell 1927).

Carrick (1983) listed the present status as common, but vulnerable because of the very specialised niche which *Ornithorhynchus* occupies. On the world's driest continent, the demand of a growing population for water for recreation, industry, drinking, irrigation and generation of hydroelectric power mounts each year. All of these activities have the potential to affect the habitat of the Platypus. Grant (1981) discussed the possible impacts of the construction of dams on the Platypus and stressed the need to include the species in the process of environmental impact assessment.



Individuals are drowned in various types of nets and traps used by fishermen, both legal and illegal (Burrell 1927; Fleay 1980; Beumer, Burbury & Harrington 1981). Meshing of eel nets to prevent entry and the setting of fyke nets with the tops of one or two hoops above the water surface, have reduced mortality in both commercial and research activities. The use of gill, mesh and trammel nets is still a problem.

## BIOGEOGRAPHY AND PHYLOGENY

### Distribution

From around Cooktown in the north of Queensland to Tasmania, the Platypus is common in lakes, rivers and creeks east of the Great Dividing Range. The distribution west of this range is poorly known and may be discontinuous. Apparently, it does not occur in westerly flowing rivers in the north of Queensland, but does so in the south of the State and in the tributaries of the Murray-Darling System in New South Wales and the Australian Capital Territory (Griffiths 1978; Stone 1983). It has been recorded in rivers over most of Victoria, including the Murray River to downstream of its confluence with the Darling (Griffiths 1978; Hampton *et al.* 1982; R.M. Warneke, Victorian Fisheries and Wildlife, personal communication). Sightings in South Australia now are restricted to occasional ones in the Murray River (Griffiths 1978). Carrick (1983) was of the opinion that the species is extinct in that State. It is common throughout Tasmania (Temple-Smith 1973; P. Murrell, Tasmanian National Parks and Wildlife Service, personal communication).

### Fossil Record and Phylogeny

*Obdurodon insignis*, a fossil species from the mid-Miocene, has been attributed to the family Ornithorhynchidae (Woodburne & Telford 1975; Archer *et al.* 1978). Recently, the ultrastructure of the teeth of *Obdurodon insignis* and *Ornithorhynchus anatinus* has been described in detail and possible phylogenetic relationships with other mammalian groups have been discussed (Lester & Archer 1986; Lester & Boyde 1986). The phylogenetic affinities of the Ornithorhynchidae are discussed in Chapter 14.

An opalised fossil of a right dentary fragment with  $M_{1-3}$  in place has been attributed to *Steropodon galmani*, an ornithorhynchid-like monotreme pre-dating *Ornithorhynchus* by more than 85 million years (Archer *et al.* 1985).

## COLLECTION AND PRESERVATION

### Collection

Specimens are normally captured by use of unweighted, multi-filament fishing nets supported by floats (Grant & Carrick 1974). Weighted nets are used in areas where there is some current, but these are less efficient at capturing animals and increase the risk of drownings. Monofilament nets, especially those which sink below the water surface and follow bottom contours, have been found to cause the most drownings, as trapped animals must attempt to lift the whole net to the surface. With floating and unweighted nets, animals can readily swim to the surface with part of the net. Box, drum and fyke nets, with wings to direct foraging animals into the entrance funnel, have been used successfully (Fleay 1980), but part of the trap must protrude above the water at all times.

### Laboratory Care

Platypuses have been kept in captivity and exhibited to the public for many years (Collins 1973; Carrick *et al.* 1982), although only one has been bred in captivity (Fleay 1944). Grant, Williams & Carrick (1977) described maintenance of animals under laboratory conditions. In all of these situations the animals have been housed in complexes consisting of nest boxes connected to feeding and/or display tanks by artificial tunnels. Food items given successfully to captive individuals include live earthworms, mealworms, freshwater crayfish and mosquito fish, as well as saltwater prawns and various egg custard mixes.

Captive mortality is high (Grant *et al.* 1977; McColl 1983). Some individuals, however, take to captivity readily and have lived for over 12, and up to 17 years in a zoo situation (Carrick *et al.* 1982). Eleven months is the longest period an individual has been kept under laboratory conditions. This animal was released at the end of that time. Others have been kept for 3–4 months and have been recaptured in good health after their release back into the wild (Grant 1984; Grant *et al.* 1977).

### CLASSIFICATION

*Obdurodon insignis* (extinct)

*Ornithorhynchus anatinus* (Shaw, 1799)

### LITERATURE CITED

- Aleksiuk, M. & Baldwin, J. (1973). Temperature dependence of tissue metabolism in monotremes. *Canadian Journal of Zoology* 51: 17–19
- Andres, K.H. & von Düring, M. (1984). The platypus bill. A structural and functional model of pattern-like arrangement of different cutaneous sensory receptors. Pp. 81–89 in Hammann, N. & Iggo, A. (eds) *Sensory Receptor Mechanisms*. World Scientific Publications Co. : Singapore
- Archer, M., Flannery, T.F., Fitchie, A. & Molnar, R.E. (1985). First Mesozoic mammal from Australia – an early Cretaceous monotreme. *Nature* 318: 363–366
- Archer, M., Plane, M.D. & Pledge, N. (1978). Additional evidence for interpreting the Miocene *Obdurodon insignis* Woodburne and Tedford, 1975, to be a fossil platypus (Ornithorhynchidae: Monotremata) and a reconsideration of the status of *Ornithorhynchus agilis* De Vis, 1885. *Australian Zoologist* 20: 9–28
- Augee, M.L. (1976). Heat tolerance in monotremes. *Journal of Thermal Biology* 1: 181–184
- Augee, M.L. & Ealey, E.H.M. (1968). Torpor in the echidna, *Tachyglossus aculeatus*. *Journal of Mammalogy* 49: 446–454
- Baldwin, J. & Aleksiuk, M. (1973). Adaptation of enzymes to temperature: lactate and malate dehydrogenases from platypus and echidna. *Comparative Biochemistry and Physiology* 44B: 363–367
- Barnett, C.H., Harrison, R.J. & Tomlinson, J.D. (1958). Variation in the venous system of mammals. *Biological Review* 33: 442–487
- Beumer, J.P., Burbury, M.E. & Harrington, D.J. (1981). The capture of fauna other than fish in eel and mesh nets. *Australian Wildlife Research* 8: 673–678
- Bohringer, R.C. (1981). Cutaneous receptors in the bill of the platypus (*Ornithorhynchus anatinus*). *Australian Mammalogy* 4: 93–106

- Bohringer, R.C. & Rowe, M.J. (1977). The organisation of the sensory and motor areas of the cerebral cortex in the platypus (*Ornithorhynchus anatinus*). *Journal of Comparative Neurology* 174: 1–14
- Briggs, E.A. (1936). The red blood corpuscles of primitive mammals. *Nature* 138: 762
- Brightman, V.J. (1976). The vallate foliate papilla complex and suckling behaviour. *Anatomical Record* 184: 363–364
- Burrell, H. (1927). *The Platypus*. Angus & Robertson : Sydney 227 pp.
- Caldwell, W.H. (1884b). On the development of the monotremes and ceratodus. *Proceedings of the Royal Society of New South Wales* 18: 117–122
- Campbell, C.B.G. & Hayhow, W.R. (1972). Primary optic pathways in the duckbill platypus, *Ornithorhynchus anatinus*. *Journal of Comparative Neurology* 145: 195–208
- Canfield, P.J. & Whittington, R.J. (1983). Morphological observations on the erythrocytes, leucocytes and platelets of free-living platypuses, *Ornithorhynchus anatinus* (Shaw) (Ornithorhynchidae: Monotremata). *Australian Journal of Zoology* 31: 421–432
- Carrick, F.N. (1983). Platypus *Ornithorhynchus anatinus*. Pp 4–6 in Strahan, R. (ed.) *The Australian Museum Complete Book of Australian Mammals*. The National Photographic Index of Australian Wildlife. Angus & Robertson : Sydney
- Carrick, F.N. & Hughes, R.L. (1978). Reproduction in male monotremes. *Australian Zoologist* 20: 211–231
- Carrick, F.N., Grant, T.R. & Williams, R. (1982). Platypus *Ornithorhynchus anatinus*: its captive maintenance. Pp 4–12 in Evans, D.D. (ed.) *The Management of Australian Mammals in Captivity*. Zoological Parks Board of Victoria : Melbourne
- Chauvet, J., Hurpet, D., Michel, G., Chauvet, M.-T., Carrick, F.N. & Archer, R. (1985). The neurohypophyseal hormones of the egg-laying mammals: identification of arginine vasopressin in the platypus (*Ornithorhynchus anatinus*). *Biochemical and Biophysical Research Communications* 127: 277–282
- Collins, L.R. (1973). *Monotremes and Marsupials, a Reference for Zoological Institutions*. D.C. : Smithsonian Institution Press : Washington D.C. vi 323 pp.
- Dawson, T.J., Grant, T.R. & Fanning, D. (1979). Standard metabolism of monotremes and the evolution of homeothermy. *Australian Journal of Zoology* 27: 511–515
- Dowd, D.A. (1969b). The coronary vessels and conducting system in the heart of monotremes. *Acta Anatomica* 74: 547–573
- Dunnet, G.M. & Mardon, D.K. (1974). A monograph of Australian fleas (Siphonaptera). *Australian Journal of Zoology Supplementary Series* 30: 1–273
- Durette-Desset, M.-C. & Cassone, J. (1983). A taxonomic revision of the trichostrongyloid nematode parasites of the echidna, *Tachyglossus aculeatus* (Monotremata). *Australian Journal of Zoology* 31: 257–284
- Eadie, R. (1935). Hibernation in the platypus. *Victorian Naturalist* 52: 71–72
- Faragher, R.A., Grant, T.R. & Carrick, F.N. (1979). Food of the platypus (*Ornithorhynchus anatinus*) with notes on the food of the brown trout (*Salmo trutta*) in the Shoalhaven River, New South Wales. *Australian Journal of Ecology* 4: 171–179
- Fleay, D. (1944). *We Breed the Platypus*. Robertson & Mullens : Melbourne 44 pp.

- Fleay, D. (1980). *Paradoxical Platypus*. Jacaranda Press : Brisbane 150 pp.
- Flynn, T.T. & Hill, J.P. (1939). The development of the Monotremata IV. Growth of the ovarian ovum, maturation, fertilization and early cleavage. *Transactions of the Zoological Society of London* 24: 445–622
- Gates, G.R., Saunders, J.C., Bock, G.R., Aitken, L.M. & Elliott, M.A. (1974). Peripheral auditory function in the platypus, *Ornithorhynchus anatinus*. *Journal of the Acoustical Society of America* 56: 152–156
- Grant T.R. (1984). *The Platypus*. University of New South Wales Press : Kensington 76 pp.
- Grant, T.R. (1981). Platypuses and dams – questions and hypotheses. Pp 206–218 in Riney, T. (ed.) *Wildlife Management in the 80's*. Monash University : Clayton
- Grant, T.R. (1982). Food of the platypus, *Ornithorhynchus anatinus* (Monotremata: Ornithorhynchidae), from various water bodies in New South Wales. *Australian Mammalogy* 5: 235–236
- Grant, T.R. (1983a). Body temperatures of free-ranging platypuses, (Monotremata), with observations on their use of burrows. *Australian Journal of Zoology* 31: 117–122
- Grant, T.R. (1983b). The behavioural ecology of monotremes. Pp 360–394 in Eisenberg, J.F. & Kleiman, D.G. (eds) *Advances in the Study of Mammalian Behavior*. American Society of Mammalogists, Special Publication No. 7
- Grant, T.R. & Carrick, F.N. (1974). Capture and marking of the platypus, *Ornithorhynchus anatinus* in the wild. *Australian Zoologist* 18: 133–135
- Grant, T.R. & Carrick, F.N. (1978). Some aspects of the ecology of the platypus, *Ornithorhynchus anatinus* in the upper Shoalhaven River, New South Wales. *Australian Zoologist* 20: 181–199
- Grant, T.R. & Dawson, T.J. (1978a). Temperature regulation in the platypus, *Ornithorhynchus anatinus*, maintenance of body temperature in air and water. *Physiological Zoology* 51: 1–6
- Grant, T.R. & Dawson, T.J. (1978b). Temperature regulation in the platypus, *Ornithorhynchus anatinus*, production and loss of metabolic heat in air and water. *Physiological Zoology* 51: 315–332
- Grant, T.R. & Griffiths, M. (1984). Aspects of lactation in the platypus, *Ornithorhynchus anatinus*. *Australian Mammal Society Bulletin* 8: 120
- Grant, T.R. & Temple-Smith, P.D. (1983). Size, seasonal weight change and growth in the platypus, *Ornithorhynchus anatinus* (Monotremata: Ornithorhynchidae) from the rivers and lakes of New South Wales. *Australian Mammalogy* 6: 51–60
- Grant, T.R., Griffiths, M. & Leckie, R.M.C. (1983). Aspects of lactation in the platypus (*Ornithorhynchus anatinus*) in waters of New South Wales. *Australian Journal of Zoology* 31: 881–889
- Grant, T.R., Williams, R. & Carrick, F.N. (1977). Maintenance of the platypus (*Ornithorhynchus anatinus*) in captivity under laboratory conditions. *Australian Zoologist* 19: 117–123
- Green, H.L.H. (1930). A description of the egg tooth of *Ornithorhynchus* with some notes on the development of the palatine processes of the premaxillae. *Journal of Anatomy* 64: 512–522
- Green, H.L.H. (1937). The development and morphology of the teeth of *Ornithorhynchus*. *Philosophical Transactions of the Royal Society of London B* 288: 367–420
- Green, J. (1984). Tie me *Ornithorhynchus anatinus* down sport. *Geo* 6: 90–105



- Griffiths, M.E. (1978). *The Biology of Monotremes*. Academic Press : New York x 367 pp
- Griffiths, M.E. (1984). Mammals: monotremes. Pp. 351–385 in Lamming, G.E. (ed.) *Marshall's Physiology of Reproduction Vol. 1*. Churchill Livingstone : Edinburgh 4<sup>th</sup> edn
- Griffiths, M.E., Green, B., Leckie, R.M.C., Messer, M. & Newgrain, K.W. (1984). Constituents of platypus and echidna milk with particular reference to the fatty acid complement of the triglycerides. *Australian Journal of Biological Science* 37: 323–329
- Hampton, J.W.F., Howard, A.E., Poynton, J. & Barnett, J.L. (1982). Records of the Mammal Survey Group of Victoria 1966–1980, on the distribution of terrestrial mammals in Victoria. *Australian Wildlife Research* 9: 177–202
- Hanström, B. & Wingstrand, K.G. (1951). Comparative anatomy and histology of the pituitary in the egg-laying mammals, the Monotremata. *Lunds Universitets Årsskrift N.F. Avd. 2 Bd 47 Nr. 6*: 1–39
- Harrop, C.J.F. & Hume, I.D. (1980). Digestive tract and digestive function in monotremes and macropod marsupials. Pp 63–77 in Schmidt-Nielsen, K., Bolis, L. & Taylor, C.R. (eds) *Comparative Physiology: Primitive Mammals*. Cambridge University Press : Cambridge
- Hickman, V.V. (1955a). *Maritrema ornithorhynchi* sp.n. A new trematode from the monotreme *Ornithorhynchus anatinus* (Shaw) with a key to the genus *Maritrema* (Nicoll). *Revista Ibérica de Parasitología. Tomo extraordinario*. Marzo 1955 : Granada (España)
- Hill, W.C.O. & Rewell, R.E. (1954). The caecum of monotremes and marsupials. *Transactions of the Zoological Society of London* 28: 185–240
- Hines, M. (1929). The brain of *Ornithorhynchus anatinus*. *Philosophical Transactions of the Royal Society of London B* 217: 155–287
- Hochstetter, F. (1896). Beiträge zur Anatomie und Entwicklungsgeschichte des Blutgefäßsystems der Monotremen. *Denkschriften der Medizinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 5: 191–231
- Home, E. (1802a). A description of the anatomy of the *Ornithorhynchus paradoxus*. *Philosophical Transactions of the Royal Society of London* 1802: 67–84
- Howell, A.B. (1937). The swimming mechanism of the platypus. *Journal of Mammalogy* 18: 217–223
- Hughes, R.L. & Carrick, F.N. (1978). Reproduction in female monotremes. *Australian Zoologist* 20: 233–253
- Hulbert, A.J. & Grant, T.R. (1983a). A seasonal study of body condition and water turnover in a free-ranging population of platypuses, *Ornithorhynchus anatinus* (Monotremata). *Australian Journal of Zoology* 31: 109–116
- Hulbert, A.J. & Grant, T.R. (1983b). Thyroid hormone levels in an egg-laying mammal, the platypus, *Ornithorhynchus anatinus*. *General and Comparative Endocrinology* 51: 401–405
- Hyrtl, J. (1853). Das arterielle Gefasssystem der Monotremen. *Denkschriften der Kaiserlichen Akademie der Wissenschaften* 5: 1–20
- Iredale, T. & Troughton, E. (1934). A checklist of mammals recorded from Australia. *Memoirs of the Australian Museum* 6: i–xii, 1–122
- Isaacks, R., Nicol, S., Sallis, J., Zeidler, R. & Kim, H.D. (1984). Erythrocyte phosphates and haemoglobin function in monotremes and marsupials. *American Journal of Physiology* 15: R236–241
- Johansen, K., Lenfant, C. & Grigg, G.C. (1966). Respiratory properties of the blood and response to diving of the platypus, *Ornithorhynchus anatinus* (Shaw). *Comparative Biochemistry and Physiology* 18: 597–608

- Kim, H.D., Baird, M., Sallis, J., Nicol, S. & Isaacks, R.E. (1984). Active cation transport and (sodium, potassium, magnesium) -ATPase of the monotreme erythrocytes. *Biochemistry and Physiology Research Communications* 119: 1161–1167
- Krause, W.J. (1971). Brunner's glands of the duck-billed platypus (*Ornithorhynchus anatinus*). *American Journal of Anatomy* 132: 147–166
- Krause, W.J. (1975). Intestinal mucosa of the platypus *Ornithorhynchus*. *Anatomical Record* 181: 251–265
- Lester, K. & Archer, M. (1986). A description of the molar enamel of a middle Miocene Monotreme (*Obdurodon*, Ornithorhynchidae). *Anatomy and Embryology* 174: 145–151
- Lester, K. & Boyde, A. (1986). Scanning microscopy of platypus teeth. *Anatomy and Embryology* 174: 15–26
- Luckett, W.P. (1976). Fetal membranes of the Monotremata and the origin of mammalian viviparity. *Anatomical Record* 184: 466
- Mackerras, J.J. (1959). Catalogue of Australian mammals and their recorded internal parasites. I-IV. Part I. Monotremes and Marsupials (pp. 101-125). Part II. Eutheria (pp. 126-143). Part III. Introduced Herbivora and the Domestic Pig (pp. 143-153). Part IV. Man (pp. 153-160). *Proceedings of the Linnean Society of New South Wales* 83: 101-160
- Mackerras, M.J. (1959). The Haematozoa of Australian mammals. *Australian Journal of Zoology* 7: 105–135
- Martin, C.J. (1902). Thermal adjustment and respiratory exchange in monotremes and marsupials. A study in the development of homeothermism. *Philosophical Transactions of the Royal Society of London B* 195: 1–37
- Mawson, P.M. (1973). Amidostomarinae (Nematoda: Trichostrongyloidea) from Australian marsupials and monotremes. *Transactions of the Royal Society of South Australia* 97: 257–279
- McCull, K.A. (1983). Pathology of captive platypuses (*Ornithorhynchus anatinus*) in Victoria, Australia. *Journal of Wildlife Disease* 19: 118–122
- McCull, K.A. & Whittington, R.J. (1985). Leptospiral titres in wild platypuses (*Ornithorhynchus anatinus*) in New South Wales. *Australian Veterinary Journal* 62: 66–67
- McDonald, I.R. (1978). Adrenocortical function in monotremes. *Australian Zoologist* 20: 79–85
- Messer, M., Gadiel, P.A., Ralston, G.B. & Griffiths, M. (1983). Carbohydrates of the milk of the platypus. *Australian Journal of Biological Sciences* 36: 129–137
- Montagna, W. & Ellis, R.A. (1960). Sweat glands in the skin of *Ornithorhynchus paradoxus*. *Anatomical Record* 137: 271–277
- Munday, B.L. & Peel, B.F. (1983). Severe ulcerative dermatitis in platypus. *Journal of Wildlife Diseases* 19: 257–279
- Murtagh, C.E. (1977). A unique cytogenetic system in monotremes. *Chromosoma (Berlin)* 65: 37–57
- Newell, F.W. (1954). The eye and ocular adnexa of the monotreme *Ornithorhynchus anatinus*. Pp. 501–554 in, *Transactions of the Royal Ophthalmological Society*, 1953. Columbia University Press : New York
- Nicholls, A.G. (1958). The population of a trout stream and the survival of released fish. *Australian Journal of Marine and Freshwater Research* 9: 320–350

- Parer, J.T. & Metcalfe, J. (1967a). Respiratory studies of monotremes. 1. Blood of the platypus (*Ornithorhynchus anatinus*). *Respiratory Physiology* 3: 136–142
- Poland, H. (1892). *Fur-bearing Animals in Nature and Commerce*. Gurney & Jackson : London
- Poulton, E.B. (1885). On the tactile terminal organs and other structures in the bill of *Ornithorhynchus*. *Journal of Physiology*, London 5: 15–16
- Pridmore, P. (1978). Locomotion and locomotor evolution in monotremes. Unpublished M.Sc. Thesis, Monash University : Clayton
- Pridmore, P. (1985). Terrestrial locomotion in monotremes (Mammalia: Monotremata). *Journal of Zoology*, London 205: 53–74
- Richards, G.C. (1986). Predation on a platypus, *Ornithorhynchus anatinus* (Monotremata: Ornithorhynchidae), by a goshawk. *Australian Mammalogy* 9: 67
- Roberts, F.H.S. (1970). *Australian Ticks*. CSIRO : Melbourne iii 267 pp.
- Robinson, K.W. (1954). Heat tolerances of Australian monotremes and marsupials. *Australian Journal of Biological Science* 7: 348–360
- Scheich, H., Langner, G., Tidemann, C., Coles, R.B. & Guppy, A. (1986). Electroreception and electrolocation in the platypus. *Nature* 319: 401–402
- Schultz, W. (1967). Die Blutgefäßversorgung des Magen-Darmkanals der Monotremen. *Zeitschrift für Anatomie und Entwicklungsgeschichte* 126: 303–319
- Smyth, D.M. (1973). Temperature regulation in the platypus, *Ornithorhynchus anatinus* (Shaw). *Comparative Biochemistry and Physiology* 45A: 705–715
- Stearns, S.C. (1976). Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3–47
- Stone, G.C. (1983). *Distribution of the platypus (Ornithorhynchus anatinus) in Queensland*. Queensland National Parks and Wildlife Service : Brisbane 55 pp.
- Strahan, R. & Thomas, D.E. (1975). Courtship of the platypus, *Ornithorhynchus anatinus*. *Australian Zoologist* 18: 165–178
- Temple-Smith, P.D. (1973). Seasonal breeding biology of the platypus, *Ornithorhynchus anatinus* (Shaw 1799) with special reference to the male. Unpublished PhD Thesis, Australian National University : Canberra 261 pp.
- Temple-Smith, P.D. & Grant, T.R. (1982). Spur structure and development in the platypus. *Bulletin of the Australian Mammal Society* 7: 47
- Walls, G.L. (1942). *The Vertebrate Eye and its Adaptive Radiation*. Cranbrook Institute of Science Bulletin No. 19. Hills, Cranbrook Press : Michigan 785 pp.
- Weiss, M. (1973). Biosynthesis of adreno-cortical steroids by monotremes, echidna (*Tachyglossus aculeatus*) and platypus (*Ornithorhynchus anatinus*). *Journal of Endocrinology* 58: 251–262
- Whittington, R.J. & Grant, T.R. (1983). Haematology and blood chemistry of the free-living platypus, *Ornithorhynchus anatinus* (Shaw). (Monotremata: Ornithorhynchidae). *Australian Journal of Zoology* 31: 475–482
- Whittington, R.J. & Grant, T.R. (1984). Haematology and blood chemistry of the conscious platypus, *Ornithorhynchus anatinus* (Shaw) (Monotremata: Ornithorhynchidae). *Australian Journal of Zoology* 32: 631–635
- Whittington, R.J. & McColl, K.A. (1983). Aspiration pneumonia in a wild platypus, *Ornithorhynchus anatinus*. *Australian Veterinary Journal* 60: 277

- Woodburne, M.O. & Tedford, R.H. (1975). The first tertiary monotreme from Australia. *American Museum Novitates* 2588: 1–11
- Yamada, J. & Krause, W.J. (1983). An immunological survey of endocrine cells and nerves in the proximal small intestine of the platypus, *Ornithorhynchus anatinus*. *Cell and Tissue Research* 234: 153–164