MAMMALIAN SPECIES No. 585, pp. 1–9, 3 figs.

Ornithorhynchus anatinus.

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Published 1 June 1998 by the American Society of Mammalogists

Ornithorhynchus Blumenbach, 1800

Platypus Shaw, 1799. Not *Platypus* Herbst, 1793.
Ornithorhynchus Blumenbach, 1800:205. Type species *Ornithorhynchus paradoxus* Blumenbach [=*Platypus anatinus* Shaw, 1799:no.118]
Dermipus Wiedemann, 1800:180.

CONTEXT AND CONTENT. Order Monotremata, Family Ornithorhynchidae. *Ornithorhynchus anatinus* is a single living genus and species (Nowak, 1991; Groves, 1993). No subspecies currently are recognized.

Ornithorhynchus anatinus Shaw, 1799
Platypus

Platypus anatinus Shaw, 1799: plate 385.
Ornithorhynchus anatinus Shaw, 1799:10. Type locality "Australia, New South Wales, New Holland (=Sydney)."
Ornithorhynchus paradoxus Blumenbach, 1800:205. Type locality coast region of New South Wales.
Ornithorhynchus fuscus Péron, 1807: Tab. 34, fig. 1. Type locality coast region of New South Wales.
Ornithorhynchus rufus Péron, 1807: Tab. 34, fig. 2. Type locality coast region of New South Wales.
Ornithorhynchus crispus Macgillivray, 1827:128. Type locality "Tasmania."
Ornithorhynchus laevis Macgillivray, 1825:132. No type locality (Thomas, 1923:177).
Ornithorhynchus paradoxi Meckel, 1826. Different spelling of *O. paradoxus.*
Ornithorhynchus brevirostris Ogilby, 1832:150. Type locality "Swan River."
Ornithorhynchus novaehollandiae Lacépède, 1800:78. Type locality New Holland (=Sydney).
Ornithorhynchus phoxinus Thomas, 1923:176. Type locality "Dinner Creek, Rauenshoe, 2900′," North Queensland.
Ornithorhynchus triton Thomas, 1923:178. Type locality "West of the great dividing range, in the drainage-area of the Darling and Murray Rivers."

DIAGNOSIS. *Ornithorhynchus anatinus* (Fig. 1) is the only living semiaquatic monotreme. It shares the order Monotremata with only the short-beaked echidna, *Tachyglossus aculeatus,* from Australia, and the long-beaked echidna, *Zaglossus bruijni,* from New Guinea (Groves, 1993). This species is unique in having a soft, pliable, and rubbery bill, which only superficially resembles the bill of a duck (Carrick, 1995). Dentition is unconventional: infants have milk teeth which are shed without replacement, whereas adults have horny grinding plates and shearing ridges. Skeletal structure is similar to that of other mammals, but interclavicle and precoracoid bones in the pectoral girdle and rudimentary ribs on the cervical vertebrae bear similarity to the skeleton of reptiles (Grant, 1995). The tail of the platypus appears to resemble the tail of a beaver (*Castor canadensis*); however, the former is lightly furred and not scaled (Grant, 1995). The male platypus also is distinctive in having a horny spur on each rear ankle. These hollow spurs are connected by ducts to venom glands located in the thigh region. As in birds and reptiles, the reproductive, excretory, and digestive systems open into a cloaca. Like other monotremes, the platypus lays eggs instead of bearing live young (Grant, 1995).

FIG. 1. *Ornithorhynchus anatinus* (courtesy of P. A. Pridmore, Canberra, Australia).

GENERAL CHARACTERS. The platypus gives the appearance of several animals combined into one (Griffiths, 1988). It is characterized by a soft duck-like bill with a frontal shield, two nostrils located on top of the bill, and with the small eyes and ears housed in grooves located on either side of the head. Limbs of the platypus are short. The forefeet are webbed and have broad nails, whereas the hind feet are partially webbed and have sharp claws. Adult males have spurs on the inside of their hind feet. The furred tail is broad and flat (Griffiths, 1988). With the exception of its bill and feet, the body of the platypus is covered in soft, dense, waterproof fur. Coat color is medium to dark brown on the dorsal side, and rufous-brown to silvery-gray on the ventral side (Griffiths, 1978). Females lay eggs, and the young are incubated outside the body. Females have no teats but have mammary glands and suckle their young (Grant, 1995).

The skull of the platypus is highly distinctive (Fig. 2). The maxilla and premaxilla are two elongated pairs of bones that support the soft tissue of the upper bill. A single pair of elongated dentary bones supports the lower bill. In young platypuses, the skull houses small teeth and stubby roots, whereas in adults dentition consists of flattened, horny plates (Grant, 1995; Griffiths, 1988).

The body is elongate and streamlined like other amphibious mammals such as otters (*Lutra* =*Lontra canadensis* and *Enhydra lutris*) and beavers, and is well suited for its semi-aquatic mode of life (Collins, 1973; Grant, 1995). It is slightly larger than the native Australian water rat (*Hydromys chrysogaster*) but relatively small compared with many amphibious mammals (Grant, 1995). Platypuses exhibit sexual dimorphism, with males being larger than females. The means and ranges for body dimensions (in mm) for males and females, respectively are as follows: total length, 500, 450–600 and 430, 390–550; tail length, 125,105–152 and 112, 85–130; bill length, 58, 49–70 and 52, 45–59 (Grant, 1995). Size varies with location, but a north-south clinal difference is not apparent. Measurements of total length (mm) and mass (g, *SD*, where available) for males and females, respectively, from different parts of Australia are as follows: North Queensland, 44.1 ± 3.1, 1018 ± 208 and 41.0 ± 1.8, 704 ± 49; Southeast Queensland, 49.3 ± 2.7, 1556 ± 194 and 43.8 ± 1.6, 1222 ± 94; New South Wales, east of divide, 50.5 ± 2.4, 1434 ± 218 and 41.5 ± 2.0, 857 ± 107; New South Wales, on divide, 47.4 ± 3.5, 1379 ± 32 and 40.3 ± 2.0, 888 ± 92; New South Wales, west of divide, 54.9 ± 29, 2215 ± 364 and 47, 2000; and Tasmania, 53.2, 1900 and 53.5, 1500 (Carrick, 1995).

DISTRIBUTION. The platypus is found in freshwater

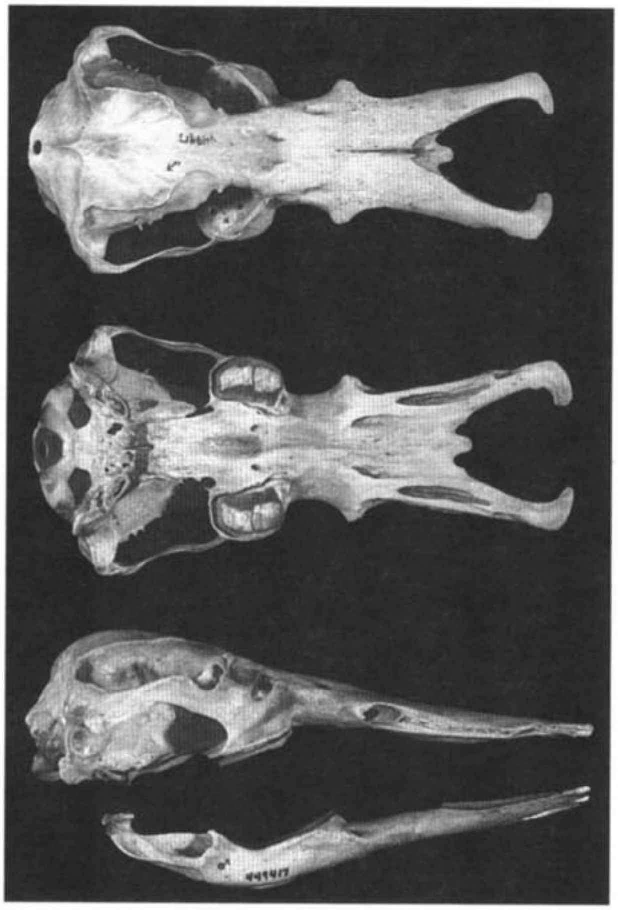

FIG. 2. Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Ornithorhynchus anatinus* (National Museum of Natural History, 449417, male, Derwent River, Tasmania, Australia). Greatest length of skull is 107.5 mm.

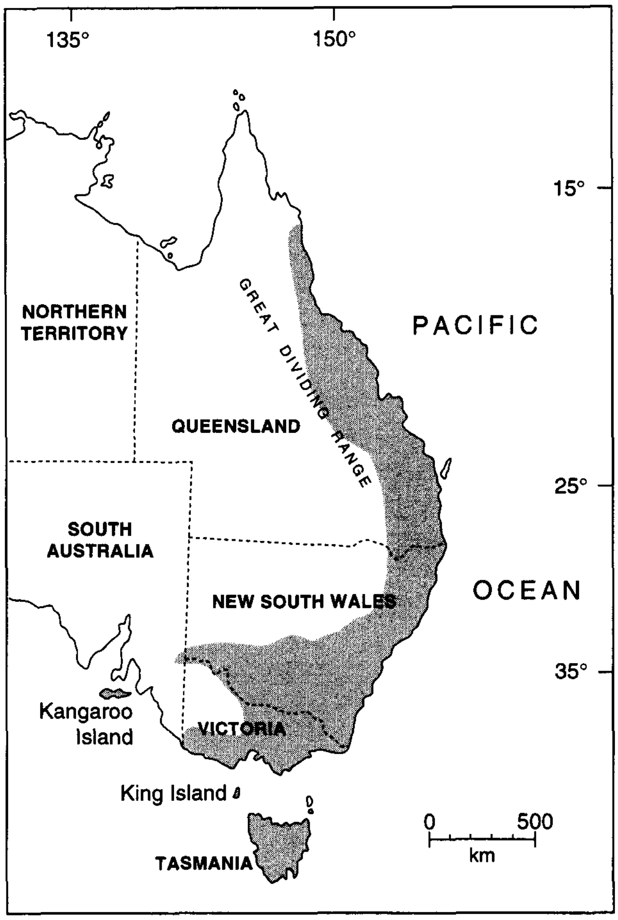

FIG. 3. Geographic distribution of *Ornithorhynchus anatinus* in Australia and Tasmania (Grant, 1992*a*, 1995).

streams, lakes, and lagoons of eastern Australia including Queensland, New South Wales, Victoria, South Australia, and Tasmania (Grant, 1995; Griffiths, 1988; Groves, 1993; Fig. 3). In northern Queensland, platypuses occur in east-flowing river systems, whereas in southern Queensland, New South Wales, and Victoria, the species is found west of the Great Dividing Range. The species does not occur west of the Divide in northern or central Queensland, in the Gulf of Carpentaria, or in the Lake Eyre Drainage Divisions (Grant, 1992*a*). The distribution of the platypus shows remarkable flexibility in both habitat choice and adaptability to a wide range in temperature. The species is able to cope successfully in both the hot tropical rainforests of Queensland and in the snow-covered mountain areas of New South Wales (Grant, 1995). Overall, the current distribution and abundance of the platypus has changed little since white settlement in Australia, and the species continues to occupy most of its historical range (Grant, 1992*a*, 1995).

In Queensland, New South Wales, Victoria, and Tasmania, historic and current distributions are similar. In Victoria, numbers have declined around the Melbourne metropolitan areas. Platypuses were introduced on Kangaroo Island between 1929 and 1946, and the populations are still active today. The species also inhabits King Island, but apparently is absent from the islands of the Furneaux Group (Grant, 1992*a*). In South Australia, historic records suggest that the platypus has always been relatively uncommon. In 1990, a platypus was sighted in the Murray River, near Renmark. The species is rare in the Murray valley, and likely extinct in the Mount Lofty Ranges/Fleurieu Peninsula area (Grant, 1992*a*).

FOSSIL RECORD. Although fossils of Ornithorhynchids are known in Australia dating back 130×10^6 years ago, fossil remains of the platypus are extremely rare (Strahan, 1995). A piece of lower jaw containing three molar teeth belonging to an ornithorhynchid-like monotreme was recovered from early Cretaceous sediments at Lightning Ridge, New South Wales (Archer et al., 1985). This fossil, named *Steropodon galmani*, is the oldest known monotreme, tentatively placed in the family Ornithorhynchidae. Its discovery indicates the antiquity of the Monotremata (Archer et al., 1985).

A skull, partial dentary, and nearly complete non-vestigial upper and lower dentitions of an extinct platypus, *Obdurodon dicksoni*, was discovered from Oligo-Miocene deposits at Riversleigh, northwestern Queensland (Archer et al., 1992). The skull of *O. dicksoni* is larger and more plesiomorphic than the skull of the living *O. anatinus*. Well-developed and functional teeth in *O. dicksoni* suggest that loss of teeth in the monotremes may have been a relatively recent event. Most fossils were recovered from a site dominated by aquatic vertebrates, suggesting that *O. dicksoni* was probably aquatic just like *O. anatinus* (Archer et al., 1992).

A Miocene genus, *Obdurodon insignis*, was discovered in South Australia. Close morphological resemblance between *Obdurodon* and *Ornithorhynchus* justifies assigning the fossil to the family Ornithorhynchidae (Archer et al., 1978; Woodburne and Tedford, 1975).

FORM AND FUNCTION. The bill of the platypus is covered with soft and naked skin. Histological examination of the bill shows it to be made up of a thick layer of keratinized epidermal tissue enclosing a vascular dermis surrounding a central core of bone. Two specialized epidermal structures, rod organs and ducts of glands within the reticular layer of dermis, are associated with sensory functions (Bohringer, 1992). Rod organs are distributed throughout the epidermis of the bill but are most concentrated on its upper border. Position and orientation of the intraepidermal nerves of the rod organs and their attachment to the epidermal cells enables these terminals to act as mechanoreceptors (Andres and von During, 1984). Innervated glands are believed to be the electroreceptors. The platypus has one serous and two mucus-secreting glands (Andres and von During, 1984, 1988). The serous and one mucus-secreting gland contain nerve terminals at the base of the ducts, whereas the second mucus-secreting gland is not innervated. The innervated mucus glands lie in a longitudinal orientation on the bill surface and are interspersed with non-innervated mucus glands. Innervated serous glands are located on external and internal surfaces of the bill, but are concentrated mostly at the border of the bill and on buccal specializations (Andres and von During, 1984, 1988).

Electro- and mechanoreceptors enable the platypus to navigate and locate prey under water. Movements by small, bottom-dwelling invertebrates generate weak electric currents which stimulate electroreceptors of the platypus (Scheich et al., 1986). As the bill encounters an electric field, the signal is a rapidly changing voltage gradient (Proske et al., 1992). Mechanoreceptors respond to tactile stimulation by prey, resulting in the platypus capturing its prey (Scheich et al., 1986). In the platypus, electroreceptors are supplied by the trigeminal (fifth cranial) nerve and the frequency of voltage fluctuations is 140 Hz (Gregory et al., 1987). Platypuses do not have a peripheral synapse (Gregory et al., 1989). Due to the wide dynamic range of its electroreceptors, the platypus may detect a lot of detail in murky waters (Gregory et al., 1988). When on land, the mucous gland associated with the electroreceptors helps preserve conductivity and prevent damage by desiccation (Scheich et al., 1986).

The bones of the upper and lower jaws expand distally, providing support for the bill (Nowak, 1991). A reduction in the olfactory system, also observed in many water-adapted mammals, likely occurred with the concomitant specialization of the trigeminal system and the electric sense (Zeller, 1988).

Juvenile platypuses have small calcified teeth with little enamel and numerous stubby roots. Juveniles also have degenerate molars that are replaced by flattened horny plates in adults (Griffiths, 1988). The dental formula is i 0/5, c 1/1, p 2/2, m 3/3, total 34 (Marshall, 1984). The plates are sharp ridges near the front of the mouth, but become flat towards the back and function as crushing surfaces. Food is crushed and ground between the horny plates, which grow throughout the life of the animal (Nowak, 1991). The grit taken up with food probably acts as an abrasive to aid in mastication (Collins, 1973). Serrations in the skin along the margins of the lower jaw likely are used for sorting food particles as food is ground by the horny pads. The tongue is short and rough with two small projections at its base and works against the palate to aid with mastication (Grant, 1995).

The skeleton of the platypus is streamlined and well adapted for swimming, burrowing, and walking. The shoulder girdle is similar to that of modern reptiles and has a T-shaped interclavicle bone. Attached to the pelvic girdle are two epipubic bones similar to those in marsupials; their function is unknown. The platypus has rudimentary ribs on the cervical vertebrae, reminiscent of reptiles; however, the seven vertebrae are a unique mammalian characteristic (Grant, 1995). The limbs are short and stout to support large muscles, and the webbed feet each have five clawed digits. Soles are naked and no distinct plantar pads are present (Marshall, 1984). In swimming, diving, and digging, the forefeet are used more than the hind feet. During terrestrial locomotion, the platypus walks on its knuckles, whereas echidnas walk on their palms. In contrast to echidnas, the body of the platypus is less elevated and at low speeds contacts the substratum (Pridmore, 1985). When walking or burrowing, the webs of the forefeet are turned back, exposing broad nails (Griffiths, 1988). The hind feet are partially webbed and are used as rudders in water, whereas the claws provide good traction in burrowing (Griffiths, 1988).

The platypus is endothermic and homeothermic (Grant, 1983; Grant and Dawson, 1978*a*, 1978*b*). Fluctuations in body temperature are greater in wild than in captive individuals (Grant, 1983; Grant and Dawson, 1978*a*; Grigg et al., 1992); nevertheless, the mean body temperature of free-ranging animals resting in thermoneutral conditions is ca. 32.1 ± 0.3°C (Grant, 1983). Platypuses in the wild spend up to 51% of the day foraging in water at temperatures as low as 0°C in winter (Grant, 1983). Normal body temperature is maintained by adjusting metabolic rate. The platypus exhibits an increase in metabolism of 1.8 times the resting level in response to a drop in air temperature from 25°C to 5°C, and 3.2 times higher when immersed in cold water of 5°C (Grant and Dawson, 1978*b*). Captive animals reveal a slight increase in body temperature during exposure to cold water, which is probably due to muscular activity and restriction of heat loss due to changes in tissue conductance (Grant and Dawson, 1978*a*).

Fur of the platypus is a major physical insulator against heat loss. The body of the platypus is covered by a pelage of coarse and fine fur that is waterproof. The longer principal hairs have a flattened leaf-shape, point backwards, and lie flat on the fine hairs, thus enhancing the insulative qualities of the coat. Platypus fur has ca. 600–900 hairs /mm^2. Air is trapped by the fine kinked underfur, and the guard hairs keep the fur structure intact. Upon diving, some air is squeezed out of the fur by water pressure, but the remainder functions to help insulate the animal. Fur is thickest on the ventral surface of the body. The relatively short pelage likely is a compromise between thermoregulation and locomotion requirements. The tail is sparsely furred and acts mainly as a fat storage area; the fat acts as insulation (Grant, 1995; Griffiths, 1978).

In the platypus, the forefeet are the major organs of propulsion and make up 13.5% of the total surface area of the body; all unfurred extremities make up ca. 31.9% (Grant and Dawson, 1978*b*). In air temperatures up to 15°C, the fur provides more than half of the body's insulation, but in water it decreases to 30–40% of the value in air. Below air temperature of 15°C, tissue insulation becomes more important. The platypus appears to have evolved complex anatomical specializations in the cardiovascular system of the extremities, suggestive of a sophisticated countercurrent heat-exchange system. Use of burrows and the curled sleeping posture also are important in conserving body heat (Grant and Dawson, 1978*b*).

Evaporative heat loss is low over a temperature range of 5–30°C and is likely a consequence of low heat production in the species. Sweat glands are found over the body and bill, giving the platypus high tolerance to heat stress. Use of water and protective burrows are also means of coping with heat stress (Grant and Dawson, 1978*b*).

Seasonal changes in body condition of free-living platypuses were estimated by use of body fat content. Seasonal loss of body condition varies depending on age and sex. Seasonal fat loss is greater in juveniles than in adults. Upon emergence from burrows in summer (February), juveniles have a greater relative amount of fat compared with adults. By the end of winter, juveniles have less absolute and relative body fat than adults. Adult males show the least seasonal changes in body condition, whereas juvenile males show the greatest. Adult and juvenile females show a similar pattern, however the differences between the two groups is not as dramatic. Juvenile males are in poorest condition at the end of winter (Hulbert and Grant, 1983).

Carcass analyses of 10 platypuses (range of weight: 846–2,056 g) showed a negative correlation between percentage body fat and percentage body water, and indicated that the major storage of body fat was in the tail. Total body water makes up 63.9% ± 1.0% of the body weight; total body fat is 8.3% ± 1.0%; and tail weight is 8.3% ± 0.4%. Tail fat is 43.1% ± 3.5% of the total body fat (Hulbert and Grant, 1983). Measurements from three free-living adult platypuses showed a loss of 46 g of fat from the tail and 49 g from the total body, providing evidence that most fat loss during autumn and winter comes from the tail (Hulbert and Grant, 1983).

Diving physiology was studied in the laboratory using five platypuses captured from the wild. Most animals dove for 30–240 s. Before diving, heart rates were 140–230 beats/min, whereas after diving heart rates were 10–120 beats/min. The fall in heart rate is indicative of restricted blood supply to tissues, but the short recovery times after dives is symptomatic of little anaerobic metabolism (Evans et al., 1994). Compared to most diving mammals, platypuses exhibit low stores of myoglobin oxygen in muscles, ca. 5.6 ml/kg body weight. Estimates of available O_2 capacity and consumption rate reveal little need for anaerobic metabolism during normal dives (Evans et al., 1994). Distribution of muscle lactate dehydrogenase isozymes also is indicative of low dependence on anaerobic glycolysis, and it is likely the heart uses the path of aerobic lactate oxidation (Evans et al., 1994). Muscles of the platypus also show low buffering capacity to metabolic acids that accumulate during anaerobiosis (Evans et al., 1994).

Platypuses have high hemoglobin concentrations in their blood. Hemoglobin of the platypus has an O_2 affinity similar to that of other mammals, but its high oxygen-carrying capacity enables the animals to extract enough oxygen from oxygen-poor burrows and store sufficient oxygen for dives. The platypus has an oxygen carrying capacity of 23.0 ml O_2/100 ml of blood, 19 g hemoglobin/100 ml of blood, 10.0 million red blood cells/mm^3 of blood, and

49% volume red blood cells in the blood. This is comparable to other burrowing mammals (Grant, 1995). Sizes (mean diameter ± *SD*, with range in parentheses) of various blood cells are as follows: erythrocytes, 5.6 ± 1.6 μm (4.8–7.2); lymphocytes, 10.7 ± 2.8 μm (7.2–20.4); neutrophils, 12.3 ± 1.1 μm (9.6–14.4); monocytes, 14.9 ± 1.4μm (12.0–18.0); eosinophils, 14.5 ± 1.2 μm (13.2–16.8); basophils, 13.0 ± 0.6 μm (12.6–14.0); and platelets, mostly 2–5 μm (range 2–8—Canfield and Whittington, 1983). Light microscopy shows erythrocytes and platelets to be similar to those of other mammals. In contrast, leukocytes are unusual in having Döhle bodies within segmented neutrophils. Similarly, the non-segmented nature of the nuclei of eosinophils and basophils is unusual compared to most mammals (Canfield and Whittington, 1983).

In the platypus, no sexual dimorphism can be detected in hematological and blood chemical values; however, age-related changes are apparent. Mean erythrocyte counts are significantly higher in young juveniles (12.5×10^{12}/l) compared with older juveniles (9.6×10^{12}/l) and adults (9.7×10^{12}/l). A small intraerythrocytic parasite is found in <1% of red blood cells of each animal (Whittington and Grant, 1983).

Free-living platypuses show a high white blood cell count (mean for adults, 42.8×10^{9}/l) with lymphocytes predominating over neutrophils (Whittington and Grant, 1983, 1995). Lymphocyte count appears to be highly sensitive to stress associated with capture. In non-anesthetized animals, a reduction of 10–58% of the initial lymphocyte count (mean for adults, 27.8×10^{9}/l) results in a significant decrease in total white cell count. Death of animals occurs when lymphocyte counts drop below 5×10^{9}/l due to bacterial infection (Whittington and Grant, 1995). In contrast, individuals anesthetized with ether show increased lymphocyte counts. Thus, peripheral blood lymphocyte counts may be a useful means of monitoring stress response of newly-captured, non-anesthetized platypuses (Whittington and Grant, 1995).

Stress associated with capture also is marked by rapid increases of concentrations of plasma glucocorticoids, catecholamines, and free fatty acids. Surprisingly, mean plasma glucose concentration after capture shows only a minor and transient increase. It is probable that the platypus is less dependent on carbohydrate reserves and more dependent on mobilization of fat reserves when subjected to stress (McDonald et al., 1992). In females, seasonal influence on glucocorticoid response is highest during pregnancy and early lactation, whereas that of males is greatest prior to mating, suggesting an association between adrenal size and reproduction (McDonald et al., 1992).

As mammals age, an increase in globulin fractions results in an increase in levels of total serum and plasma protein. Compared with adults, juvenile platypuses show lower globulin and higher albumin levels, and consequently, lower serum and plasma proteins (Whittington and Grant, 1983). Growing juveniles also tend to have elevated alkaline phosphatase and inorganic phosphate levels because of higher osteoblastic activity. In platypuses, both alkaline phosphatase and inorganic phosphate levels decrease with increasing age (Whittington and Grant, 1983). Serum cholesterol levels also appear to be age-related. Juveniles trapped in January contained milk in the digestive tract and had the highest serum triglyceride levels. Juveniles captured in March contained no milk and had similar levels of serum triglycerides as adults; therefore weaning of juveniles appears to be linked to decreasing serum triglyceride levels. Possibly, high serum triglyceride levels in juveniles are associated with suckling: triglyceride levels decrease between suckling periods while cholesterol levels remain high, but after weaning cholesterol levels also decrease (Whittington and Grant, 1983).

Spurs appear to be associated primarily with breeding activity. First-year juveniles of both sexes have spurs, which degenerate in females. In males, the hollow spurs of both hind legs are ≤15 mm in length and are connected to glands which secrete a powerful venom. This venom is capable of causing excruciating pain in humans and may even result in death of animals the size of a dog (Carrick, 1995; Griffiths, 1988). Venom is produced in the crural gland and is linked to the spur via a distensible duct (Martin and Tidswell, 1985). The venom contains hyaluronidase and proteolytic activities, which are prevalent in vertebrate and arthropod venoms, as well as a natriuretic peptide, found in the venom of the green mamba snake, *Dendroaspis angusticeps* (de Plater et al., 1995). Venom is injected into other animals by the platypus driving its hind legs together and plunging the erected spurs into the target. Males use spurs in intraspecific fighting and in self-defense (Grant, 1995; Temple-Smith, 1973). Spur morphology changes over time and can be used to group male platypuses into broad age categories.

In the platypus, two separate uteri, the ureter, and the bladder enter a common urogenital sinus which opens into the cloaca. The right ovary is non-functional, so eggs develop in the ovarian follicles of the left ovary. At ca. 4 mm in diameter, the egg is passed out of the ovarian follicle and is fertilized by threadlike sperm in the beginning of the Fallopian tube. Following fertilization, the first shell layer is laid down and the egg passes out of the Fallopian tube into the uterus. Two more layers of shell are secreted by glands in the uterus; these glands also provide nutrients to the developing egg or eggs (Grant, 1995).

Mammary glands of monotremes do not have nipples like those of eutherians and metatherians. Mammary glands of most platypuses are quiescent from May to mid-July; during this time they regress and are not easily detected by the naked eye. The glands consist of a system of closed ducts invested with myoepithelium and patent lumina (Griffiths et al., 1973). By the end of July, mammary glands grow by mitotic cell division and differentiate into large fan-shaped structures which take up most of the ventral abdominal surface of the body (Grant, 1995). The connective tissue around the glands hypertrophies, becomes hypercellular, and strands of mesenchyme derived from the hypercellular tissue replace the adipose tissue present around the glands. The duct system of the glands becomes less dense, forms outgrowths near the periphery which penetrate the newly-formed connective tissue matrix, and the new solid duct system acquires lumina. When the young hatch, the tubules expand and subdivide until thin-walled alveoli with milk are formed (Griffiths et al., 1973). Special glandular cells produce milk which is secreted into ducts that collect together at the surface of the skin in two milk patches or areolae. Prodding of the milk patches by nestlings stimulates the formation of oxytocin, which results in contraction of cells in the mammary glands causing milk to be ejected onto the fur (Grant, 1995).

Milk of the platypus is creamy white in color and contains 39.1 g/100 g solids, of which 22.2% is crude lipid, 8.2% crude protein, 3.3% hexose, and 0.4% sialic acid, and a concentration of 21.1 mg/l of iron (Griffiths et al., 1984). Milk fat contains 98.5% triglycerides with the remainder being phospholipids and free fatty acids. Very small amounts of cholesterol esters are present. Polyunsaturates make up 29% of the triglyceride fatty acids in milk fat and 32% of the total fatty acids in the lipid of the food. The major polyunsaturates of both food and milk are linoleate, arachidonate, and eicosapentaenoate, whereas docosapentaenoate is present primarily in milk (Gibson et al., 1988). Platypus milk is extremely rich in protein and is similar to that of rabbits, guinea-pigs, rats, and some marsupials, but lower than that of the echidna (Teahan et al., 1991). High concentrations of iron are needed for the formation of hemoglobin in juveniles because initially the liver is underdeveloped and cannot store sufficient amounts of iron (Grant, 1995).

The monosaccharide composition of acid hydrolysates of water-soluble carbohydrates is 33% L-fucose, 29% D-galactose, 20% glucosamine, 11% D-glucose, and 7% sialic acid (Messer et al., 1983). The principal neutral carbohydrate of platypus milk is difucosyllactose, a tetrasaccharide. Free lactose occurs in trace amounts. In contrast, the principal carbohydrate of milk of placental and marsupial mammals is lactose (Messer and Kerry, 1973). Most likely, developing platypuses utilize fucose as an energy source, which is comparable to the role of milk galactose and glucose in therian mammals (Messer et al., 1983).

In the male, the penis is covered in a thin-walled preputial sac and lies ventral to the cloacal chamber. When erect, it can pass through the cloaca to the exterior through the cloacal aperture. The penis measures ca. 50–70 mm in length. The urethra carries semen, whereas urine is passed separately from the urogenital sinus into the cloaca. Testes of the platypus are testicond (Griffiths, 1978). The major androgenic compound found in spermatic venous and peripheral blood is testosterone. During the breeding and non-breeding seasons, testosterone levels in spermatic venous blood are 400 and 10 ng/ml, respectively. Similarly, in peripheral blood, concentrations of 12 and 0.3 ng/ml are observed in breeding and non-breeding seasons, respectively (McFarlane and Carrick, 1992). Testis size is positively correlated with testosterone levels. Testes of breeding and non-breeding males weigh ca. 27 and 1.7 g, respectively (Grant, 1995). Accessory glands include Cowper's glands, which are connected by ducts to the penile urethra, and disseminate tubular glands, which enclose the urogenital sinus (Griffiths, 1978).

ONTOGENY AND REPRODUCTION. Platypuses are seasonal breeders. Male testis size begins to increase in May (Temple-Smith, 1973) and plasma testosterone concentrations peak during June/July (McFarlane and Carrick, 1992), suggesting that males enter breeding condition earlier than females. Based on progesterone levels, reproductive activity begins in August and continues into September (Handasyde et al., 1992). Mating is preceded by courtship activities. Courtship behavior and mating rarely have been observed in the wild due to the secretive nature of the species. In captivity, males appear to initiate up to 90% of the interactions, but mating success depends on compliance of the female (Grant, 1995).

Males do not begin to produce sperm until the onset of their second spring, but it remains unclear if they actually breed during that season (Grant, 1995). Females typically do not breed until they are at least 2 years old (Grant and Temple-Smith, 1983; Temple-Smith, 1973), and some do not breed until their fourth year or later (Grant, 1995). It appears that adult females do not reproduce every year, and only the dominant males are successful breeders. Breeding time varies with location, occurring earliest in Queensland, later in New South Wales, and latest in Victoria and Tasmania (Grant, 1995).

Females construct nesting burrows which are used to incubate and nurse their young. Only females care for their offspring; males seem to take no part in rearing young. The exact gestation period is unknown, but it may be similar to the echidna, which is ca. 1 month (Grant, 1995). The normal number of eggs is two (range, 1–3), and the eggs measure ca. 14 by 17 mm (Burrell, 1927; Grant and Griffiths, 1992). The female likely incubates her eggs by assuming a curled posture and holding the eggs pressed to her belly with her tail. Incubation time is not known but is thought to be between six and ten days (Grant, 1995). Offspring possess a sharp egg tooth, similar to echidnas and reptiles, which enables them to tear open their rubbery shells (Griffiths, 1978, 1988). The size of a newly-hatched platypus is thought to be similar to that of the echidna, which measures ca. 15 mm in length (Grant, 1995). Similar to newborn marsupials, newborn platypuses are highly underdeveloped with rudimentary hind limbs but well developed forelimbs which are used to pull themselves up to nurse (Griffiths, 1988; Grant, 1995). Most females begin to lactate in October or November and continue for 3–4 months (Grant and Griffiths, 1992). Upon leaving the burrow, juvenile male and female platypuses are ca. 410 and 370 mm in length, respectively, which is approximately 80% of adult length, but 56–67% of adult weight (Grant, 1995). At this age, juveniles continue to nurse, although for how long is not clear. Juvenile females attain full adult size sooner than males (Grant and Temple-Smith, 1983).

ECOLOGY. Platypuses inhabit lakes, fast-flowing mountain streams, peat-stained racing streams, sluggish streams, slow-running tributaries of rivers, and lagoon-like still waters. The presence of permanent freshwater is essential to their survival, thus limiting their distribution within the Australian continent (Fleay, 1980).

Platypuses are primarily nocturnal; however, their activity pattern usually has been described as bimodal (Collins, 1973; Grant, 1992*b*; Temple-Smith, 1973). Recent work with activity recorders, however, suggests that the activity pattern of the species is more unimodal, with animals typically exiting and entering burrows once each evening (Serena, 1994). Platypuses spend up to 16 h out of the burrow, averaging 10 h/night, and are active longer through the night during summer than in winter (Grant, 1992*b*; Gust and Handasyde, 1995).

The platypus is an opportunistic feeder (Grant, 1982) and a carnivore (Grant and Carrick, 1978). Platypuses feed by swimming along bottoms of freshwater streams and lakes and probing in the mud and gravel with the highly sensitive ends of their rubbery bills (Collins, 1973). Examination of the contents of cheek pouches reveals platypus diet to be almost entirely made up of bottom-dwelling invertebrates (Trichoptera, Diptera, Coleoptera, Ephemeroptera, and Odonata), but can contain freshwater shrimp (*Paratya australiensis*), bivalve molluscs (*Sphaerium*), earthworms, tadpoles, and trout eggs (Collins, 1973; Faragher et al., 1979; Grant, 1982). Platypuses appear to be opportunistic foragers, and invertebrates tend to be taken in proportion to their numerical abundance (Faragher et al., 1979). There is some variation in food types based on locality and season (Collins, 1973). Occasionally, platypuses eat items floating on the surface of the water such as cicadas (*Melampsalta denisoni*), which often fall out of trees that line river banks (Griffiths, 1978). In both breeding and nonbreeding seasons, free-ranging platypuses spend an average of 10 h/day foraging (Gust and Handasyde, 1995; Serena, 1994). Food is stored in cheek pouches while submerged and usually masticated at the surface with sideways movements of the horny plates on the maxillae and lower jaws (Collins, 1973; Faragher et al., 1979). Bits of exoskeletons are ejected into the water through a series of horny serrations arranged along the margins of the lower jaw (Griffiths, 1978).

Platypuses occupy two types of burrows which are dug into the banks of rivers, creeks, and lake shores or are located in piles of debris that accumulate at creek channels (Burrell, 1927; Serena, 1994). Nesting burrows, used to house offspring, tend to be longer and more complex than camping or resting burrows and usually are built amongst tree roots to prevent collapse (Burrell, 1927; Grant, 1995; Serena, 1994). Nests are constructed using wet eucalyptus leaves and grass (Collins, 1973; Griffiths, 1988). Along the length of nesting burrows, females construct one or more soil plugs, each of which requires reconstruction after the female has passed through the burrow (Burrell, 1927; Griffiths, 1988; Serena, 1994). The plugs appear to be constructed as a defense against predation of offspring, as females tend to cease plugging late in juvenile development (Griffiths, 1988; Serena, 1994). Entrances to nesting burrows tend to be above the water line (Serena, 1994). Alternatively, camping or resting burrows, often have entrances below water level (Serena, 1994) and are used for protection and to avoid extreme weather (Burrell, 1927; Grant, 1983; Grant and Dawson, 1978*a*). Resting burrows tend to be used singly, but occasionally are shared (Grant et al., 1992; Serena, 1994). Platypuses also may utilize multiple nesting burrows in the same area (Burrell, 1927), with some individuals occupying 6–12 dens (Gardner and Serena, 1995).

Data on the ecology and behavior of wild platypuses largely has been collected from marked individuals. Platypuses normally are live-captured either in unweighted gill nets, which are floated parallel to a shore (Grant and Carrick, 1974), or fyke nets, which are set perpendicular to a shore (Serena, 1994). Fyke nets are extended the full width of the stream channel and to the channel bottom. Nets must be monitored frequently to minimize losses due to drowning (Grant and Carrick, 1974; Serena, 1994). When caught, individuals are marked in a variety of ways. Radio transmitters are used to document space-use, activity patterns, and fluctuations in body temperature. Transmitters have been taped (Grant et al., 1992) or glued (Gust and Handasyde, 1995; Serena, 1994) to the dorsal surface of the tail, and implanted into the peritoneal cavity (Grant et al., 1992; Grigg et al., 1992). Passive integrated transponder tags, implanted subcutaneously between the scapulae, also have been used to document space use (Grant and Whittington, 1991; Gardner and Serena, 1995). These tags are effective in identifying individuals, and remain effective for >3 years (Grant and Whittington, 1991). Platypuses also have been marked by tattooing on the ventral bill shield (Gardner and Serena, 1995) or by freeze branding (Grant and Whittington, 1991). Individuals also are tagged by use of stainless steel legbands that are attached to a hind leg (Grant and Carrick, 1974; Gust and Handasyde, 1995). Aluminum bands are less effective, as they tend to be removed by the animals (Grant and Carrick, 1978). Brightly colored adhesive tape attached to the tail also has been used to mark platypuses, although this method is effective for only a short time (Grant and Carrick, 1978).

Home range of the platypus is typically measured as a length of river normally travelled. Distances moved vary among populations, ranging from 0.37 to 2.3 km along sections of the Thredbo River, New South Wales (Grant et al., 1992) and 2.9 to 7.0 km on the Watts River and Badger Creek, Victoria (Gardner and Serena, 1995). Individuals that forage in streams have longer home ranges than those in pond habitats (Serena, 1994). Home-range areas of up to 15.5 ha for males have been recorded but are highly variable between individuals and localities (Gust and Handasyde, 1995). It is not clear if some males maintain exclusive areas during the breeding season. Evidence indicates there is a decrease in home range overlap and males appear to avoid each other with some shifting to diurnal activity, suggesting that both temporal and spatial separation exists. This likely depends on population density and habitat availability (Gust and Handasyde, 1995). Males typically overlap with more than one female (Gardner and Serena, 1995). Females do not appear to defend fixed, mutually exclusive areas (Serena, 1994). Recapture of about half of marked animals and the continuous appearance of new adults suggests that the population structure consists of both resident and transient individuals (Grant, 1995). A long-term study of 18 years indicates that the sex ratio of adults and juveniles is biased towards females (Grant and Griffiths, 1992).

Mark-recapture and radiotelemetry studies indicate that wild platypuses live to at least 12 years of age and females may still raise young at 11 years of age. In captivity, individuals have been known to live up to 22 years. After individuals reach adulthood, mortality rate appears to be low (Grant, 1995).

Little is known about mortality factors in the species, but these may include disease and floods, as well as some predation by foxes (*Vulpes vulpes*), snakes, birds of prey, feral cats, and possibly eels (Grant, 1995). As with most semiaquatic mammals, dispersal is the stage in life history when individuals are thought to be particularly vulnerable to predation, as exemplified by a predation attempt by a grey goshawk (*Accipiter novaehollandiae*) on a dispersing juvenile (Richards, 1986). Juveniles may disperse in search of new habitats to live in, or they may be forced to disperse by competition for food or burrows with resident members of the population. Currently, it is not known where juveniles disperse to. Juveniles also may suffer from mortality due to starvation and heat stress (Grant, 1995). Out of 166 juveniles captured and marked in the upper Shoalhaven River of New South Wales over a period of 18 years, only 25% had been recaptured; the rest are assumed to have either died or dispersed (Grant, 1995).

Diseases also cause mortality. The platypus is a host to a range of infectious agents, many of which appear to be well tolerated (Whittington, 1992). Internal parasites include protozoans (*Theileria ornithorhynchi, Trypanosoma binneyi, Toxoplasma, Coccidia*), a cestode (*Spirometra erinacei*), trematodes (*Mehlisia ornithorhynchi, Maritrema ornithorhynchi, Moreauia mirabilis*), and nematodes (*Cercopithifilaria johnstoni, Tasmanema mundayi*, family Cylindrocorporidae, larvae of family Trichostrongylidae, adults of subfamily Filaroidinae). Ectoparasites include fleas (*Pygiopsylla hoplia, P. zethi*), mites (family Trombiculidae), and ticks (*Amblyomma triguttatum, Ixodes ornithorhynchi*—Whittington, 1988, 1992). Juveniles often have greater infestations of ticks than adults. Concentrations ≤200 ticks/platypus have been reported (Temple-Smith, 1973). *Ixodes ornithorhynchi* is found only on the platypus and can transmit the protozoan parasite *Theileria ornithorhynchi* (Collins et al., 1986; Grant, 1995), which infects red blood cells and causes anemia and an adenovirus infection of the epithelium of the renal collecting ducts (Whittington et al., 1990). Infections can be caused by a virus (Adenovirus), bacteria (*Leptospira interrogans, Salmonella, Aeromonas hydrophila, Escherichia coli*), and fungi (*Mucor amphibiorum, Trichophyton mentagrophytes var. mentagrophytes*, Whittington, 1988, 1992). *M. amphibiorum* causes severe ulceration of the skin, and the infection can be fatal in the platypus (Obendorf et al., 1993). The disease appears to be restricted to streams and rivers in northern Tasmania (Obendorf et al., 1993). *M. amphibiorum* has not been detected in other areas of Tasmania or on the mainland (Grant, 1995). The fungus was first isolated from an Australian tree frog, but the route of infection in the platypus is not known (Obendorf et al., 1993). In contrast to the platypus, laboratory mice, rats, and guinea pigs infected with *M. amphibiorum* show no susceptibility. Since the maximum temperature at which *M. amphibiorum* grows in vitro is 36°C, its occurrence in the platypus may be due to the species' lower body temperature (32°C) compared with that of eutherian mammals (Obendorf et al., 1993).

Historically, man has been the major cause of mortality for the platypus. At the turn of the century, pelts were sought for the fur trade, almost eradicating the species (Griffiths, 1988). Skins were made into rugs and slippers, and other apparel for women. Platypuses were killed for sport and were often caught in traps set for fish. Platypuses continue to suffer mortality from unsupervised nets (Grant, 1995).

BEHAVIOR. The social system of platypuses is largely unknown. Generally, the platypus is a solitary species, but several individuals may utilize a small body of water (Carrick, 1995). Behavioral studies are difficult because the platypus is semiaquatic, mainly nocturnal, and usually occupies a burrow when not feeding. Accordingly, it is not surprising that as recently as 1995, the mating system had not been described (Gemmell et al., 1995). Mating behavior of wild platypuses rarely has been observed. In captivity, males and females touch as they swim past each other. Courtship interactions may be initiated by the female (Strahan and Thomas, 1975) or male (Hawkins and Fanning, 1992); however, females appear to initiate ca. 10% of interactions (Grant, 1995). The male grasps the end of the female's tail with his bill, and courtship may conclude in copulation (Strahan and Thomas, 1975), although tail-holding by males does not always end in copulation (Hawkins and Fanning, 1992). Prior to the receptive period, a female rejects tail-holding attempts by a male by spiralling through the water or by pulling the male through holes between logs and rocks until she frees herself, then rapidly swims away. When receptive, the female remains close to the male and when he loses his grip she remains idle until he reattaches. Once attached, the male curls his body so that his tail is under the female to one side of her tail. The male then moves forward on the female, biting the hair on her shoulder with his bill (Fleay, 1980; Hawkins and Fanning, 1992; Strahan and Thomas, 1975).

During the mating season, aggressive encounters among males have been recorded. Spurs likely are used in intraspecific fighting between males, and in the wild, the incidence of spur wounds is higher in males than females (Grant, 1995; Griffiths, 1978). In captivity, males have killed one another using their spurs (Grant, 1995). The crural system (spurs plus associated glands) may be a mechanism for ensuring spatial separation among males during breeding time (Griffiths, 1978).

Like many species of mammals, platypuses are playful animals. In the wild, juveniles have been observed playing and splashing in the water (Grant 1995). Captive youngsters have been observed rolling, wrestling and playfully biting one another in shallow water. On land, they may mouth each other with their mandibles and paw one another with their forepaws (Griffiths, 1978). The platypus has a range of vocalizations, the most common of which is a growling sound, especially when disturbed (Carrick, 1995).

GENETICS. The chromosomes are 2n = 52, consisting of 23 pairs of autosomes, 4 unpaired autosomes, and X and Y sex chromosomes (Murtagh, 1977; Wrigley and Graves, 1984). Chromosomes of the platypus exhibit a mixture of mammalian and reptilian traits. The platypus is unique in having two categories of chromosomes: macrochromosomes, that are similar to those found in other mammals and microchromosomes, that are similar to those found in reptiles (Griffiths, 1988).

During the first division of meiosis in the male, a complex chain multiple is formed similar to that in the echidna (Murtagh, 1977). The chain is made of 21 bivalents, presumably consisting of 10 elements including the X and Y chromosomes. At this time, the X and Y chromosomes are associated with small autosomal chromosomes, four unpaired and two paired (Griffiths, 1988). X-chromosome inactivation is paternal, tissue specific, and incomplete (Vandeberg et al., 1986).

Mitochondrial DNA has been isolated from toe-web tissue of the platypus (Gemmell et al., 1992). The average size of the mtDNA genome was calculated to be 16.7 Kb, which falls within the range typical for eutherian mammals. Genomic DNA digested with either the restriction endonuclease HinfI or DdeI and probed with p64.2.5.E1 and pINS310 has been used for DNA fingerprinting to determine relatedness within small populations (Gemmell et al., 1995).

CONSERVATION. At the turn of the century, the platypus was rendered almost extinct by fur-hunters (Griffiths, 1988). Currently, the platypus is protected in all Australian states and in some regions is considered common (Grant, 1995; Griffiths, 1988). Despite its protection, the platypus is vulnerable to human activities such as ongoing habitat destruction, river and stream disturbance for agriculture, industry and dam construction, pollution, trapping, and fish netting (Carrick, 1995; Kennedy, 1992). Restricted distribution and limited genetic variation within certain populations due to genetic bottlenecks encountered within their past also increase the vulnerability of the species (Gemmell et al., 1995).

Captive rearing as a safety valve against losses in the wild presently is not a viable option because the platypus rarely breeds in captivity (Collins, 1973; Dayton, 1991; Fleay, 1980; Gemmell et al., 1995). From a survey of 228 platypuses held in Australian zoos between 1934 and 1988, almost 80% died within the first year of capture (Dayton, 1991). Stress and metabolic disorders appear to be a significant underlying factors in many deaths (Dayton, 1991; McColl, 1983). Enclosures for the platypus also are complex and expensive, and few zoos have the capability to successfully maintain the species (Collins, 1973; Fleay, 1980).

REMARKS. Since its discovery, the platypus has held a fascination for zoologists and evolutionary biologists (Fleay, 1980; Gould, 1985; Griffiths, 1978). When the first dried skin of a platypus arrived in Britain around 1798, it was thought to be a fake animal which had been made by stitching together the beak of a duck and the body parts of a mammal (Grant, 1995). In 1799, the platypus was given the name *Platypus anatinus,* meaning flat-footed, duck-like animal. Unfortunately, *Platypus* had previously been used to name a group of beetles, so the scientific name was changed to *Ornithorhynchus anatinus.* Ornithorhynchus was derived from the Greek word *ornia,* meaning bird and *rhynchos,* meaning snout (Waterhouse, 1946). Early settlers called the platypus a duckbill, watermole, or duckmole, whereas the Aborigines referred to the platypus as mallingong, boondaburra, or tambreet (Grant, 1995).

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