**Ornithorhynchus anatinus.**

By Maria Pasitschniak-Arts and Lui Marinelli

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**Ornithorhynchus Blumenbach, 1800**

*Platypus Shaw, 1799. Not Platypus Herbst, 1793.*

**Ornithorhynchus Blumenbach, 1800:205. Type species *Ornithorhynchus anatinus* Shaw, 1799:2,118**

**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.

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**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 paradoxus** 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 phasianinus** Thomas, 1923:176. Type locality “Dinner Creek, Rauenschoe, 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 preconoid 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).

**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 amphibia mammals such as otters (*Lutra 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 amphibia 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 ± 206 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 ± 82 and 40.3 ± 2.0, 885 ± 92; New South Wales, west of divide, 54.9 ± 29, 2215 ± 364 and 47, 2000; and Tasmania, 53.2, 1900 and 53.3, 1500 (Carrick, 1995).

**DISTRIBUTION.** The platypus is found in freshwater
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, 1992a). 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, 1992a, 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, 1992a). In South Australia, historic records suggest that the platypus has always been relatively uncommon. In 1900, 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, 1992a).

**FOSSIL RECORD.** Although fossils of Ornithorhynchus are known in Australia dating back 130 × 10⁶ 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., 1983).

A skull, partial dentary, and nearly complete non-vestigial upper and lower dentitions of an extinct platypus, Odburodon 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, Odburodon insignis, was discovered in South Australia. Close morphological resemblance between Odburodon 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 mecanoreceptors (Andres and von Düring, 1984). Innervated glands are believed to be the electroreceptors. The platypus has one serous and two mucus-secreting glands (Andres and von Düring, 1984, 1988). The serous and one
mucous-secreting gland contain nerve terminals at the base of the ducts, whereas the second mucous-secreting gland is not innervated. The innervated mucous glands lie in a longitudinal orientation on the bulb surface and are interspersed with non-innervated mucous 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 Düring, 1984, 1986).

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 (Prechtl 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).

Electroplax, an organ of electric organs in the platypus, has small calcified teeth with little enam el and numerous stubby roots. Juveniles also have degenerate molars that are replaced by flattened horn 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. The plate is crushed and ground between the horn 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 horn plates. The tongue is short and rough with two small projections at its base and works against the palate to aid in 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 masses of the body. Despite their small size, platypuses have a body mass of 0.4 kg and can carry a 2.5 kg load without producing any observable strain (Nowak, 1991). 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 paddles in water, whereas the claws provide good traction in burrowing (Griffiths, 1988).

The platypus is endothermic and homeothermic (Grant, 1983; Grant and Dawson, 1978b, 1978c). Fluctuations in body temperature are greater in wild than in captive individuals (Grant, 1983; Grant and Dawson, 1978a; Grigg et al., 1992); nevertheless, the metabolic rates of animals resting in thermal-neutral conditions is ca. 32.1 ± 0.2°C (Grigg et al., 1983). Platypuses can sustain a temperature of 32°C, including an average of 1°C in cold water. This is a steady temperature maintained by adjusting metabolic rate. The platypus exhibits an increase in metabolism of 1.4 times the resting level in response to cold air. Body temperatures range from 22°C to 25°C, and 3.2 times higher when immersed in cold water of 5°C (Grant and Dawson, 1978b). 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, 1978c).

Fur of the platypus is a major physical insulator against heat loss. The body of the fur is composed 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 insulating qualities of the coat. Platypus fur has ca. 600-900 hairs/mm². 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 pelage is sparse and short, but a dense 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 unfurled extremities make up ca. 31.3% (Grant and Dawson, 1978b). 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, 1978b). Evaporative heat loss is low over a temperature range of 5-30°C and is likely a consequence of low heat production in the extremities. Sweat glands are found only on the paws, and the platypus has high tolerance to heat stress. Use of water and protective burrows are also means of coping with heat stress (Grant and Dawson, 1978b).

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 lost 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 (Halibut and Grant, 1985).

Carcass analyses of 10 platypuses (range of weight: 846-2,056 g) showed a negative correlation between percentage body fat and percentage body weight, and indicated that the major storage of body fat was in the tail. Total body fat makes up 63.9% ± 1.0% of body weight; total body fat range is 8.3% ± 0.4%. Tail fat is 43.1% ± 3.5% of the total body fat (Halibut 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 (Halibut 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 suggestive of little anaerobic metabolism (Evans et al., 1994). Compared to most diving mammals, platypuses exhibit lower stores of myoglobin oxygen in muscles, ca. 5.6 ml/kg body weight. Estimates of available O2 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 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 compensate for lactic acids that accumulate during anaerobic events (Evans et al., 1994).

Platypuses have high hemoglobin concentrations in their blood. Hemoglobin of the platypus has an O2 affinity similar to that of other mammals, but its high oxygen-carrying capacity enables platypuses to extract enough oxygen from oxygen-poor burrows and store significant amounts of oxygen. The platypus has an oxygen carrying capacity of 23.0 ml O2/100 ml of blood, 19 g hemoglobin/100 ml of blood, 10.0 million red blood cells/mm³ 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 (4.9–7.2); lymphocytes, 10.7 ± 2.8 μm (7.2–20.4); neutrophils, 12.3 ± 1.1 μm (9.6–14.4); monocytes, 14.9 ± 1.4 μm (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 2.4–8). (Canfield and Whittington, 1983).

In the platypus, the urogenital sinus 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 ovary and is fertilized by a spermatozoon 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).

Mammalian glands of monoteromes do not have nipples like those of eutherians and metatherians. Mammalian 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 hypervascular, and strands of mesenchyme derived from the hypervascular 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 are in the subside uterus, the nipples are engorged, and milk is 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 the 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, 5.3% hexose, and 0.4% acid casein, and a concentration of 21.1 mg/I of iron (Griffiths et al., 1984). Milk fat contains 93.7% 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 milk of the food. The major polyunsaturates of both food milk are linoleate, arachidonate, and eicosapentaenoate, whereas docosapentaenoate is present primarily in milk (Gibson et al., 1988). Platyus 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., 1979). High concentrations of fat, protein, and minerals also tend to increase 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-glucosamine, 11% D-glucose, and 7% galactose (Messier et al., 1983). The principal neutral carbohydrate of platypus milk is d-fucosylactose, a tetrasaccharide. Free lactose occurs in trace amounts. In contrast, the principal carbohydrate of milk of placental and marsupial mammals is lactose (Messier and Kerry, 1975). Most likely, developing platypuses utilize fucose as an energy source, which is comparable to the role of milk galactose and glucose in therian mammals (Messier 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 testisoid (Griffiths, 1978). The major androgenic hormone found in the size of a dog (Carrick, 1995; Griffiths, 1988). Venon is produced in the crural gland and is linked to the spat via a distensible duct (Martin and Tidswell, 1985). The venon contains hyaluronidase and proteolytic activities, which are prevalent in vertebrate and arthropod venoms, as well as proteins associated with the venom of the green mamba snake, Dendroaspis angusticeps (de Plater et al., 1995). Venon is injected into other animals by the platypus driving its hind legs together and plunging the erected spurs into the target. Males use spars 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 groups.
which are connected by ducts to the penile urethra, and disseminate tubular glands, which enclose the urogenital sinus (Griffiths, 1978).

**ONTOMETRY 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 approach to initiate copulation, 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 unless 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 be in rearing young, but the location of the young 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 hunched 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, 1992b; 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 per night (Serena, 1994). Platypuses spend up to 16 h out of the burrow, averaging 10 h/night, and are active longer throughout the year during summer than in winter (Grant, 1992b; Gust and Handasyde, 1995).

The platypus is an opportunistic feeder (Grant, 1982) and a carnivore (Grant and Carrick, 1978). Platypuses feed by swimming along 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 Hemiptera) that contain freshwater shrimp (Paratya australasiae), bivalve molluscs (Spaerium), 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 location and season (Collins, 1973). Occasionally, platypuses feed items floating on the surface of the water such as caddis (Melanipalpa denisonii), 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 horn-like serrations arranged along the margins of the lower jaw (Griffiths, 1978).

Types of burrows occur in 70% of the nesting sites, but burrows may occur wherever the flat male platypuses can be found. Nesting burrows are used to house offspring, tend to be longer and more complex than camping or resting burrows, and usually are built among tree roots to prevent collapse (Burrell, 1927; Grant, 1995; Serena, 1994). Nesting burrows used to house offspring, tend to be longer and more complex than camping or resting burrows, and usually are built among tree roots to prevent collapse (Burrell, 1927; Grant, 1995; Serena, 1994). Nesting burrows tend to be used the above the water line (Serena, 1994). Alternates used for resting, often having entrances at water level (Serena, 1994) and are used for protection and to avoid extreme weather (Burrell, 1927, Grant, 1983; Grant and Dawson, 1978a). 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; Grant and Handasyde, 1995). 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 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 freshwater stream type, 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 individuals maintain exclusive use of a 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 usually do not defend territories (excluding territories of males) (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 to 22 years. After sexual maturation and reaching 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 novaebelaudi) 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 (NSW) from 1979 to 1982, 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, 1982). Internal parasites include protozoans (Theileria ornithorhynchi, Trypanosoma minui, Toxoplasm, Coccidia), a cestode (Spiromeris erinacei), trematodes (Meliisia ornithorhynchi, Maritrema ornithorhynchi, Moorea nazanini), and nematodes (Cercocephalidae johnstoni, Tasmanema mandravi, family Cylindrocoeliidae, family Trichosternogidae, adults of subfamily Filaroidae). Ectoparasites include fleas (Ptygiopsylla hoplia, P. sethi), mites (family Trombiculidae), and ticks (Amblyomma triguttatum, Isodes ornithorhynchi.—Whittington, 1982, 1992). Juveniles often have greater infestations of ticks than adults. Concentrations ≥200 ticks/platypus have been reported (Temple-Smith, 1973). Isodes ornithorhynchi is found only on the platypus and can transmit the protozoan parasite Theileria ornithorhynchi (Collins et al., 1980; Grant, 1995), which infects red blood cells and causes anaemia and an adenovirus infection of the epidermis collecting duct (Grant et al., 1982). Infections can be caused by a virus (Adenovirus), bacteria (Listeria intercellularis, Salmonella, Aeromonas hydrophila, Eschericia coli), and fungi (Mucor amphihorburnum, Trichophyton mentagrophytes var. mentagrophytes, Whittington, 1988, 1992). M. amphihorburnum 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. amphihorburnum 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. amphihorburnum show no susceptibility. Since the maximum temperature at which M. amphihorburnum grows in vitro is 30°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, and in 1863-1864, the platypus was exploited for its medical properties, including its blood as a source of Azotemia, such as urotherapy, the treatment of various diseases, such as arthritis, by injection into the body with the resulting decrease in the viscosity of the blood (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 so little is known about platypus behavior (Gosselin 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 courtship behaviors (Grant, 1995). The male grasps the end of the female's tail with his bill, and copulation may conclude in copulation (Strahan and Thomas, 1975), although tail-bending by males does not always end in copulation (Hawkins and Fanning, 1992). Prior to the receptive period, a female rejects tail-bending attempts by a male by spraying 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 determinant of mating success. For example, a period of 11 years during which only 25% had been recaptured; the rest are assumed to have either died or dispersed (Grant, 1995).

Like many species of mammals, platypuses are playfull animals. In the wild, juveniles have been observed playing and splashing in the water (Grant 1995). Captive youngsters have been observed rolling, wrestling and playing with one another in the water. On land, they may moult 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 growing 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; Wrigli 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 by pairing homologues at the telomeres of the chromosomes (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 HinI or DdeI and probed with p64.2.5.E1 and pNS310 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, 1888). 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 predation by cats, raccoons, and other predators, and diseases such as urotherapy, the treatment of various diseases, such as arthritis, by injection into the body with the resulting decrease in the viscosity of the blood (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).

Capture 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 1984 and 1988, almost 80% died within the first year of captivity (Dayton, 1991). Stress and metabolic disorders appear to be a significant underlying factor 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 *ornis*, meaning bird and *rhynchos*, meaning snout (Waterhouse, 1946). Early settlers called the platypus a duckbill, watermelon, or duckmelon, whereas the Aborigines referred to the platypus as mallogong, boondoburra, or tambreet (Grant, 1995).

**LITERATURE CITED**


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MARIA PASITSCHNIK-ARTS, DEPARTMENT OF BIOLOGY, UNIVERSITY OF SASKATEWAN, 112 SCIENCE PLACE, SASKATOON, SK CANADA S7N 5E2. LUI MARINELLI, ALBERTA RESEARCH COUNCIL, POST OFFICE BAG 4000, VEGREVILLE, AB CANADA T9C 1T4.