



The platypus: evolutionary history, biology, and an uncertain future

GILAD BINO,*^{1,2} RICHARD T. KINGSFORD, MICHAEL ARCHER, JOANNE H. CONNOLLY, JENNA DAY, KIMBERLY DIAS, DAVID GOLDNEY, JAIME GONGORA, TOM GRANT, JOSH GRIFFITHS, TAHNEAL HAWKE, MELISSA KLAMT, DANIEL LUNNEY, LUIS MIJANGOS, SARAH MUNKS, WILLIAM SHERWIN, MELODY SERENA, PETER TEMPLE-SMITH, JESSICA THOMAS, GEOFF WILLIAMS, AND CAMILLA WHITTINGTON

Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia (GB, RTK, MA, TG, TH, LM, WS)

School of Animal and Veterinary Sciences, Charles Sturt University, Locked Bag 588, Wagga Wagga, New South Wales, Australia (JHC)

Graham Centre for Agricultural Innovation, Wagga Wagga, New South Wales, Australia (JHC)

Sydney School of Veterinary Science, Faculty of Science, The University of Sydney, Sydney, New South Wales, Australia (JD, KD, J. Gongora, CW)

Charles Sturt University, Locked Bag 588, Wagga Wagga, New South Wales, Australia (DG)

Cesar Australia, Melbourne, Victoria, Australia (J. Griffiths)

Biological Sciences, Monash University, Melbourne, Victoria, Australia (MK)

School of Life and Environmental Sciences, The University of Sydney, Sydney, New South Wales, Australia (DL, CW)

Office of Environment and Heritage, P.O. Box 1967, Hurstville, New South Wales, Australia (DL)

School of Biological Sciences, University of Tasmania, Tasmania, Australia (SM)

Forest Practices Authority, Private Bag 5, Hobart, Tasmania, Australia (SM)

Australian Platypus Conservancy, P.O. Box 22, Wiseleigh, Victoria, Australia (MS, GW)

Department of Obstetrics and Gynaecology, Southern Clinical School, Monash University, Clayton, Victoria, Australia (PT-S)
Healesville Sanctuary, Healesville, Victoria, Australia (JT)

* Correspondent: gilad.bino@unsw.edu.au

The platypus (*Ornithorhynchus anatinus*) is one of the world's most evolutionarily distinct mammals, one of five extant species of egg-laying mammals, and the only living species within the family Ornithorhynchidae. Modern platypuses are endemic to eastern mainland Australia, Tasmania, and adjacent King Island, with a small introduced population on Kangaroo Island, South Australia, and are widely distributed in permanent river systems from tropical to alpine environments. Accumulating knowledge and technological advancements have provided insights into many aspects of its evolutionary history and biology but have also raised concern about significant knowledge gaps surrounding distribution, population sizes, and trends. The platypus' distribution coincides with many of Australia's major threatening processes, including highly regulated and disrupted rivers, intensive habitat destruction, and fragmentation, and they were extensively hunted for their fur until the early 20th century. Emerging evidence of local population declines and extinctions identifies that ecological thresholds have been crossed in some populations and, if threats are not addressed, the species will continue to decline. In 2016, the IUCN Red Listing for the platypus was elevated to "Near Threatened," but the platypus remains unlisted on threatened species schedules of any Australian state, apart from South Australia, or nationally. In this synthesis, we review the evolutionary history, genetics, biology, and ecology of this extraordinary mammal and highlight prevailing threats. We also outline future research directions and challenges that need to be met to help conserve the species.

Key words: Australia, conservation management, freshwater biology, Monotremata, *Ornithorhynchus anatinus*

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Fig. 1.—A platypus, *Ornithorhynchus anatinus* returning back to the Upper Tarago River in Victoria, Australia after having been measured and tagged. Photo by Doug Gimesy.

The platypus (*Ornithorhynchus anatinus*) is one of five extant species of egg-laying mammals in the subclass Monotremata and the only living species within the family Ornithorhynchidae (Fig. 1). As one of the world's most evolutionarily distinct mammals, the platypus has long been regarded to be of exceptional scientific importance as well as a globally unique component of Australia's biodiversity. The modern platypus is endemic to eastern mainland Australia, Tasmania, and adjacent King Island, with a small introduced population on Kangaroo Island, South Australia (Fig. 2). Platypuses are widely distributed in permanent river systems from tropical to alpine environments. However, relatively little is known about the species' past and present distribution and numbers, limiting accurate evaluation of its conservation status and future population trajectories. Recent documented local declines and extinctions identify that the species is facing considerable threats in some areas (Lintermans 1998; Lunney et al. 1998; Serena et al. 1998; Rohweder and Baverstock 1999; Otley 2001; Milione and Harding 2009). However, estimates of population sizes are particularly difficult to obtain, given low recapture rates and the substantial effort required (Grant 2004a; Serena and Williams 2012a). In South Australia, the species is nearly extinct and is "Endangered" (National Parks and Wildlife Act 1972). The current drivers of declining platypus distribution and population are many, widespread, and synergistic, including predominantly regulation of river flows (Kingsford 2000; Grant and Fanning 2007) and extensive riparian and lotic habitat degradation by land clearing for agriculture and urbanization

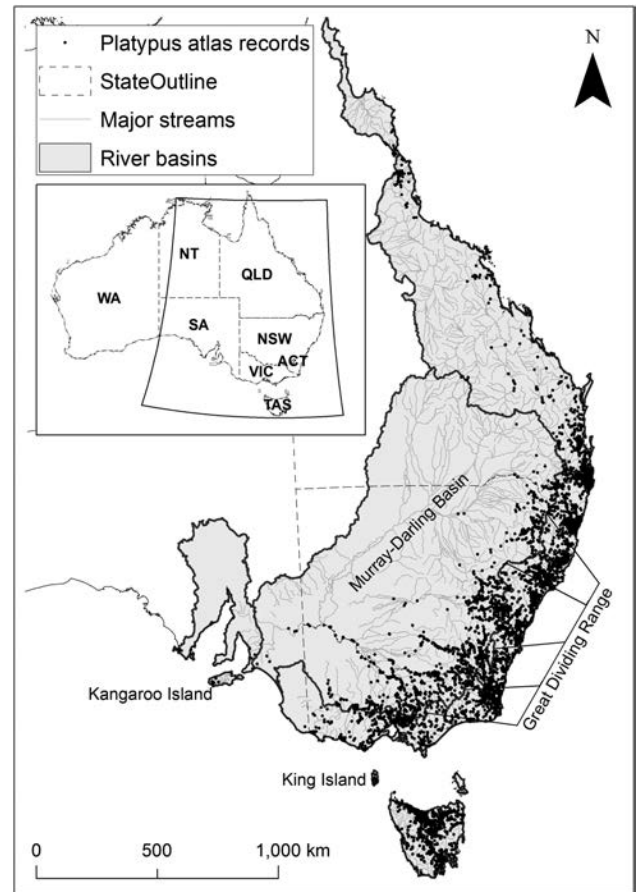


Fig. 2.—Distribution of the platypus (*Ornithorhynchus anatinus*) based on 11,830 records from Australian state government fauna atlases and the Atlas of Living Australia (www.ala.org.au) between 1760 and 2017.

(Grant and Temple-Smith 2003). In light of documented local declines, the conservation status of the platypus was elevated by the IUCN to "Near Threatened" in 2016 (Woinarski and Burbidge 2016). Given the extent and severity of the threatening processes, coupled with lack of knowledge of past and present trends, there is an urgent need to re-assess the conservation status of the species and establish a national monitoring program. Apart from South Australia, platypuses are not currently listed on the threatened species schedules of any Australian state or nationally (i.e., Environment Protection and Biodiversity Conservation Act 1999). In this synthesis, which was initiated during a workshop attended by many of Australia's platypus researchers, we review the current knowledge of the platypus' life history and identify threats to its existence, priorities for conservation, and research challenges required to conserve this unique species. Prior to assessing these topics, we provide a summary of Aboriginal knowledge and use of the species.

ABORIGINAL KNOWLEDGE AND USE

Platypuses have many Aboriginal names including Mallangong, Tambreet, Gaya-dari, Boonaburra, and Lare-re-lar (Pike 1997; McKay et al. 2001). They were hunted for food (Marshall 1992;

Cosgrove and Allen 2001) by digging them from their burrows or spearing them while swimming (Robinson and Plomley 2008), providing a food resource rich in polyunsaturated fats (Naughton et al. 1986), particularly important in cold conditions (Marshall 1992; Cosgrove and Allen 2001). Aboriginal people had also developed a deep biocultural or ecological knowledge of platypuses, which was largely overlooked by early naturalists. A dreamtime story of the platypus from the upper reaches of the Darling River (McKay et al. 2001) begins with a young duck who disregarded her tribe's warning of Mulloka (or Waaway), the water devil (Pike 1997). The duck, venturing down the creek far from her tribe, was abducted by Biggoon, a large water-rat who took the duck as his wife. The duck eventually escaped and returned to her tribe, where she laid two eggs which hatched as platypuses. They had soft fur instead of feathers, four webbed feet instead of two, and spurs on their hind legs, like Biggoon's spear. The duck and her two different children were banished by her tribe, choosing to live far away in the mountains where she could hide from her tribe and Biggoon. A second dreaming from the Central Coast in New South Wales (McKay et al. 2001) begins with the Ancestor Spirits deciding on totems. The birds, marsupials, and fish each implore the platypus to join their particular family. After consulting with the echidna, the platypus graciously declines, explaining that it shares traits with all groups and wishes to remain friends with all of them, rather than belong to one single group. The platypus commemorates the Great Spirit for making all the animals different and respecting its wisdom.

RESEARCHING THE PLATYPUS

After Europeans first encountered platypuses in 1797, several specimens arrived in Britain and Europe, prompting taxonomic description (Shaw 1799) and anatomical studies (Griffiths 1978; Hobbins 2015), including the confirmation of functional

mammary glands (Meckel 1823). Despite strong evidence for oviparity, including Aboriginal knowledge, the idea was strongly resisted by the conservative establishment as it supported the theory of transformism in nature along with all its social implications (Nicol 2018). Whereas Étienne Geoffroy Saint-Hilaire argued that platypuses were egg-laying but could not possibly lactate (Geoffroy Saint-Hilaire 1829), Richard Owen the pre-eminent comparative anatomist for much of the 19th century and the leading authority on the anatomy of monotremes and marsupials, argued that they lactated but could not possibly lay eggs. Early ideas of evolution, or transformism, were attractive to radical thinkers, whereas social conservatives were anxious to show that the boundaries between types of animals, just like the boundaries between social classes, were erected by God and could not be crossed (Nicol 2018). Owen's continued denial of oviparity was likely the most important of many impediments to conclusively settling the nature of monotreme reproduction and scientific acceptance of oviparity (Caldwell 1884; Nicol 2018).

In the late 19th and early 20th century, platypuses were widely hunted for fur and sport. They were legally protected in all states by 1912 (Victoria—1892; New South Wales—1901; Queensland—1906; Tasmania—1907; South Australia—1912), stimulating considerable study of their natural history (Burrell 1927; Barrett 1944; Fleay 1944). Studies of reproduction, physiology, ecology, and behavior began in the 1970s (Temple-Smith 1973; Grant 1976; Griffiths 1978) and gained pace in the 1990s and early 2000s (Augee 1992; Grant 1995; Manger and Pettigrew 1998; Temple-Smith and Grant 2001), while health-related studies emerged in the 1980s (Munday and Peel 1983; Whittington and Grant 1983; Fig. 2). Dedicated symposia and special issues in peer-reviewed journals from 1978 to 2009 provided publication outlets for platypus-focused research, coinciding with peaks in peer-reviewed papers (Fig. 3). The surge in research in the 21st century was driven by more researchers and

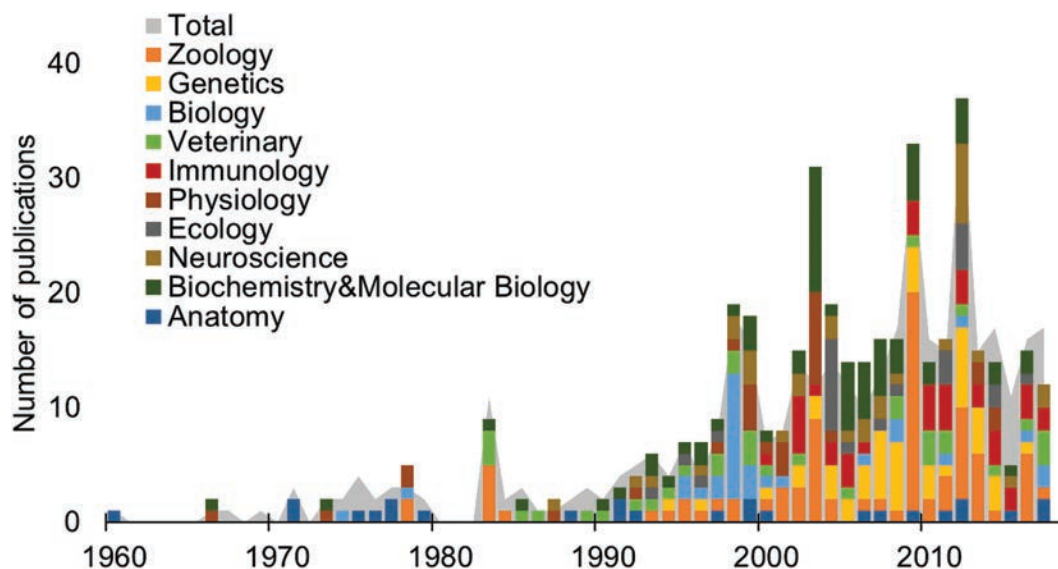


Fig. 3.—The number of peer-reviewed publications (gray fill, $n = 404$) on the platypus (*Ornithorhynchus anatinus*) grouped by year (1960–2017) and stratified by the top ten research areas (color bars) in the Web of Science database with “*Ornithorhynchus anatinus*” in either title, abstract, keywords, or keywords plus (<https://www.isiknowledge.com>).

new technological developments, including smaller telemetry and data logging devices, use of passive integrated transponder tags (“microchipping”) for permanent marking (Grant and Whittington 1991), as well as DNA technologies and sequencing (Warren et al. 2008; Martin et al. 2018; Fig. 3). A study of familial relationships marked the beginning of research using the species’ DNA (Gemmell et al. 1992, 1995). Investigations of many aspects of biology using molecular genetic technologies quickly followed (Warren and Grützner 2009), expanding with progressive development and reduction in the cost of new technologies. In the late 1980s, studies of local, state, and national populations were sparked by interest in possible changes in the distribution or numbers of the platypus since the arrival of Europeans (Grant 1991, 1992; Grant and Denny 1991; Grant and Fanning 2007). Emergence of mucormycosis, an ulcerative skin condition in Tasmanian platypuses, also raised concern (Connolly 2009). By the mid-2000s, increasing concern about the status of local platypus populations (Woinarski et al. 2014) culminated in the IUCN raising its conservation status to “Near Threatened” in 2016 (Woinarski and Burbidge 2016).

Despite this increasing research effort, key knowledge gaps remain, particularly with regards to the species’ past and present distribution and numbers, and the impacts of threatening processes on population viability. These gaps limit our ability to assess the current status and to develop conservation strategies for safeguarding the future of platypus populations. Platypuses are cryptic, and predominantly nocturnal and crepuscular, thereby impeding investigations of distribution, numbers, health, reproduction, recruitment, and movements. Trapping platypuses is time- and labor-intensive and is highly dependent on the depth and flow of water. In deep pools (> 2 m), unweighted mesh nets, often set an hour before dark, require continuous monitoring to ensure the welfare of platypuses and non-target species (e.g., fish). Fyke nets (checked every 2–4 h and allowing unimpeded access to air) are effective in small streams, although capture rates may vary substantially by age, sex, and season, and may also be affected by learned avoidance (Serena and Williams 2012b; Griffiths et al. 2013). Mark–recapture methods that take into account detection probabilities can produce robust estimates of population size (Bino et al. 2015). Environmental DNA (Ficetola et al. 2008; Lugg et al. 2018) is now used to detect the presence of platypuses and visual survey techniques provide useful information for assessing and monitoring population activity and relative abundance (Easton et al. 2008).

Platypus movements have been investigated using capture–recapture studies (Serena and Williams 2012a), radiotracking (Grant et al. 1992; McLeod 1993; Serena 1994; Gardner and Serena 1995; Gust and Handasyde 1995; Serena et al. 1998, 2001; Otley et al. 2000), microchip implantation (Macgregor et al. 2015), and externally attached (Griffiths et al. 2013) or implanted (Grant et al. 1992; Bino et al. 2018) acoustic tags. Unlike other freshwater mammals, the use of collars or harnesses for fine-scale telemetry (GPS, radio, or acoustic) is impractical, given the high risk of strangulation or drowning as platypuses forage between submerged roots and branches

and dig their burrows between tree roots (Grant and Fanning 2007). Gluing radio and acoustic trackers to the body surface provides limited temporal data before they detach as fur regrows (Griffiths et al. 2014; Griffiths and Weeks 2015). By comparison, implanted telemetry devices (subcutaneous, intraperitoneal) can generate results for up to a year (G. Bino, pers. obs.). Subcutaneously implanted passive integrated transponders (Grant and Whittington 1991) extend tracking duration but have short detection distances (< 1 m), limiting their application to narrow streams (Macgregor et al. 2015).

Research into platypus diets is mostly based on sampling the contents of cheek pouches (Grant and Carrick 1978; Faragher et al. 1979; McLachlan-Troup et al. 2010; Marchant and Grant 2015) or analysis of captive nutrition (Thomas et al. 2018b), with more recent application of stable isotope analysis of platypus fur indicating that a combination of cheek pouch and stable isotope analyses is the most thorough approach (Klamt et al. 2016). Feeding behavior of captive platypuses indicates that preferences are shaped by prey mobility and increased energy consumption associated with preparing for and recovering from breeding (Thomas et al. 2018b). Body condition can be measured using tail volume and fur condition (Grant and Carrick 1978), but portable ultrasound devices offer new and potentially more accurate indices of body condition (Macgregor et al. 2017a). Assessing the reproductive status of females remains reliant on inducing milk let-down using injected synthetic oxytocin (Grant et al. 2004). Health assessments include external physical examination, collection of parasites, sampling excreta for reproductive hormones, corticosteroid analysis or pathogens, and sampling blood for hematology, serum biochemistry, and serology (e.g., *Mucor* enzyme-linked immunosorbent assay [ELISA], *Leptospira* serovar antibody titers—Connolly et al. 1998; Macgregor 2015; Macgregor et al. 2017b).

FOSSIL RECORD AND PHYLOGEOGRAPHY

Prior to 1971, no extinct ornithorhynchids were known. A fragment of a Pliocene platypus, *Ornithorhynchus agilis* (De Vis 1885), may be the oldest known record (~3.8 million years ago [Mya]) of the living *O. anatinus* (Archer et al. 1978). The first breakthrough came with discovery of two well-formed teeth in Oligocene (~26 Mya) clay deposits in central South Australia (Fig. 4B) named *Obdurodon insignis* (Woodburne and Tedford 1975). Subsequent discovery of a dentary fragment and an ilium confirmed the ornithorhynchid nature of this taxon (Archer et al. 1978). In 1985, teeth and a nearly complete skull (Fig. 4A and 4B) of a species named *Obdurodon dicksoni* were discovered in Middle Miocene freshwater limestones (~15 Mya) in the Riversleigh World Heritage Area, Queensland (Lester and Archer 1986; Archer et al. 1991, 1992, 1993, 2000; Musser and Archer 1998; Macrini et al. 2006; Asahara et al. 2016). A second, much larger, Riversleigh species, *Obdurodon tharalkooschild*, was later discovered (Pian et al. 2013). The Riversleigh species appears to have lived in pools within cool, temperate, lowland rainforest (Archer et al. 1995, 2000).

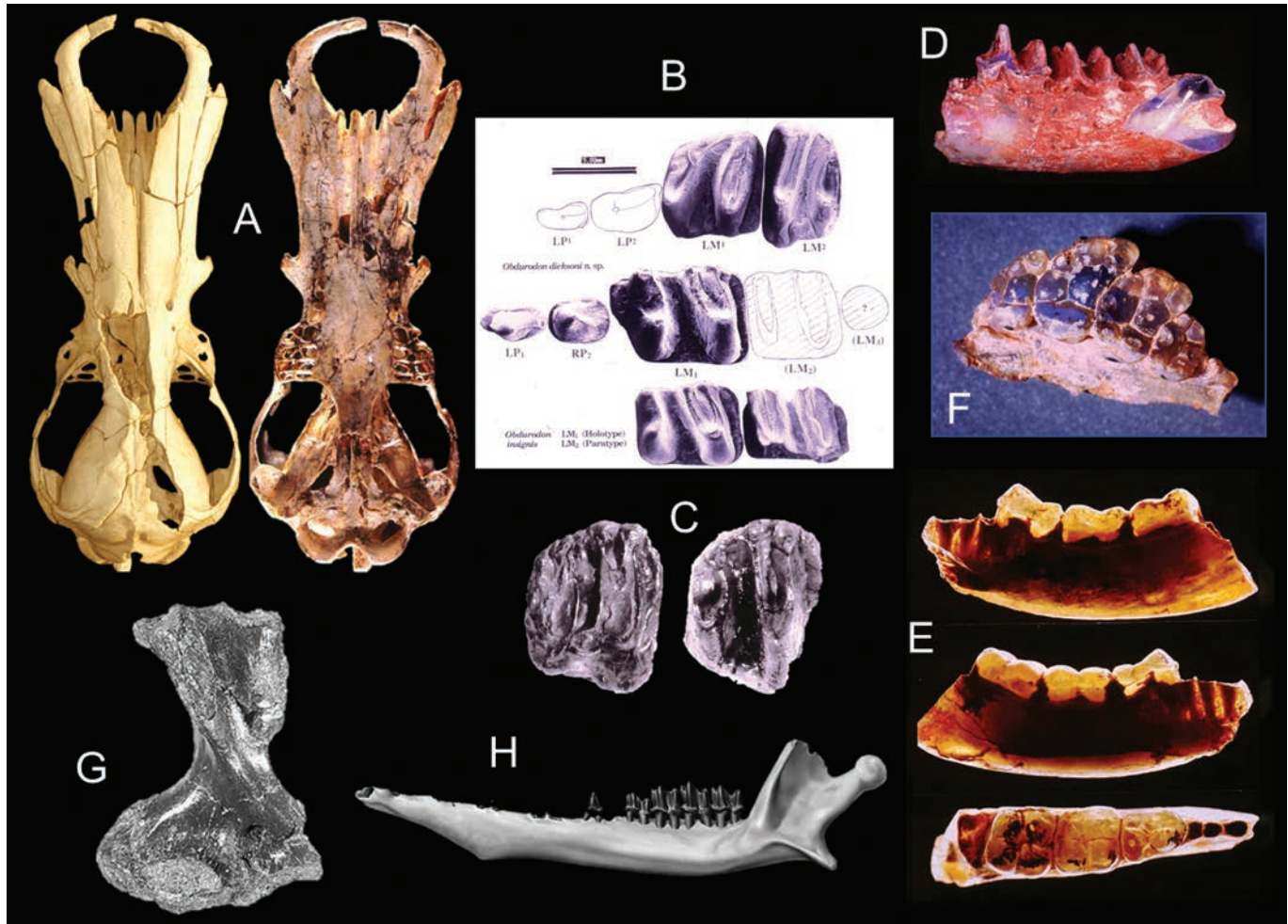


Fig. 4.—A) Dorsal and ventral views of the skull of *Obdurodon dicksoni* from Middle Miocene sediments in the Riversleigh World Heritage area (left image, dorsal view, micro-CT image courtesy T. Rowe, the University of Texas; right image, ventral view, photo Ross Arnett). B) Dentition of *O. dicksoni* (upper two rows) and *Obdurodon insignis* (bottom row—Archer et al. 1993). C) A right upper molar (RM2) of *Monotrematum sudamericanum* (left) compared with a slightly damaged RM2 (right) of *O. dicksoni* (Pascual et al. 1992b). D) Left dentary fragment with LM1–3, of *Steropodon galmani* (photo by John Field—Archer et al. 1985). E) Three views of a lower right dentary fragment with RM1–3 of *Kollikodon ritchiei*. F) Upper left maxillary fragment with LP4 to M4 of K. Ritchie (photo by John Field). G) Right humerus of *Kryoryctes cadburyi* (photo by Steven Morton—Pridmore et al. 2005). H) Left dentary of *Teinolophos trusleri* retaining one premolar (of four) and four (of five) molars (composition reconstruction by Peter Trusler—Rich et al. 2016).

With the discovery of *Monotrematum sudamericanum* (Pascual et al. 1992a, 1992b, 2002; Archer et al. 1995; Forasiepi and Martinelli 2013; Fig. 4C) from Paleocene deposits (63–61 Mya) in Argentina, it became clear that platypuses formerly existed on a continent that is now far beyond Australia (Fig. 5). Based on close overall similarity, this South American platypus could well be regarded as a species of *Obdurodon* (Musser 2013). The presence of fossils of the Queensland lungfish (*Neoceratodus forsteri*) and myobatrachid frogs in the same Patagonian deposit further demonstrated the strong faunal links that united Gondwana until at least the Eocene (about 50 Mya).

None of the older monotreme fossils now known from the Early Cretaceous (146–100 Mya) such as *Steropodon galmani*, *Kollikodon ritchiei*, *Kryoryctes cadburyi*, and *Teinolophos trusleri* (Archer et al. 1985; Flannery et al. 1995; Rich et al. 1999, 2001, 2016; Pridmore et al. 2005; Pian et al. 2016; Fig. 4D–H) have been demonstrated to be ornithorhynchids or

tachyglossids. In particular, *T. trusleri*, which appears to be the oldest known monotreme, apparently did not have a bill nor other features characteristic of ornithorhynchids. There have been arguments based on fossils and molecular data that ornithorhynchids and tachyglossids may have diverged from one another prior to the Cenozoic (Pridmore et al. 2005; Rowe et al. 2008; Springer and Krajewski 2009). However, there are counter arguments that Ornithorhynchidae may well be paraphyletic, with tachyglossids having evolved from ancestral ornithorhynchids sometime during the Cenozoic (Pascual et al. 1992b; Phillips et al. 2009). Unfortunately, because of a lack of fossil tachyglossids more plesiomorphic than the extant long-beaked (*Zaglossus* spp.) and short-beaked (*Tachyglossus aculeatus*) echidnas, uncertainty remains about the origins of echidnas and their relationships to platypuses, other than that both groups are monotremes (Camens 2010; Phillips et al. 2010; Musser 2013).

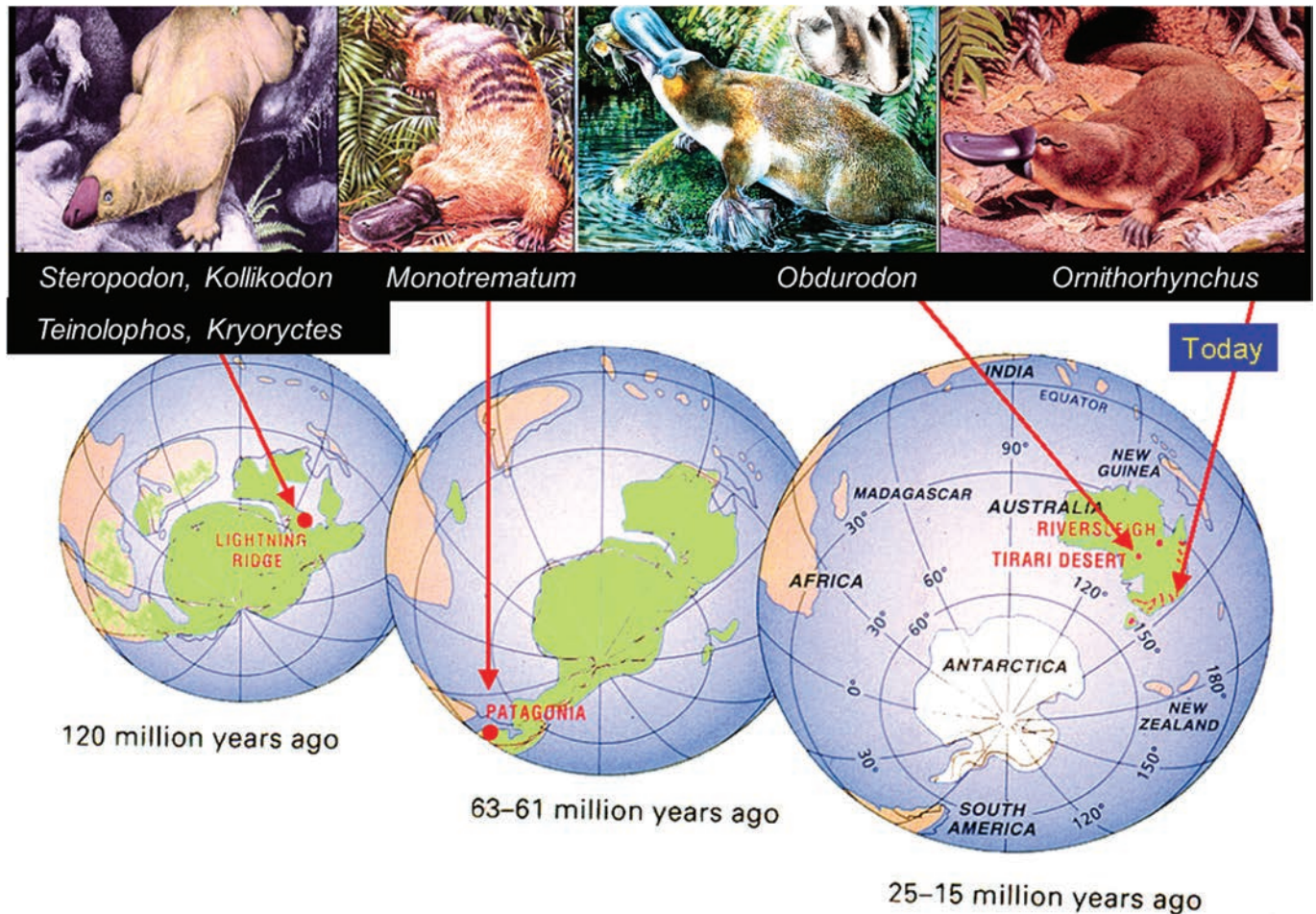


Fig. 5.—Long-term decline in geographic distribution and species' diversity in monotremes and their early descendants. Cretaceous monotremes probably occurred throughout much of eastern Gondwana. By the early Paleocene, ornithorhynchids were geographically as widespread across Gondwana as Patagonia in southern South America. By the late Oligocene/Miocene (25–15 Mya), at least three ornithorhynchids occurred across the continent of Australia but none survived on other continents. Today, the platypus (*Ornithorhynchus anatinus*) maintains an even more restricted area, the river systems of eastern Australia (modified after Archer 1995; *Steropodon* image by Peter Schouten; *Monotrematum* image by James McKinnon—Archer 1995; *Obdurodon* image by Peter Schouten—Pian et al. 2013; *Ornithorhynchus* artwork by Rod Scott, *Australian Geographic Magazine*).

Taken together (Fig. 5), the fossil record of ornithorhynchids provides a disquieting deep-time perspective on the conservation status of the living platypus that suggests that the species may be less environmentally resilient than commonly presumed. Overall, the record appears to be one of continuous geographic and taxonomic decline with representatives disappearing from Patagonia within the last 60 million years and from most of mainland Australia, apart from the relatively well-watered eastern coast, within approximately the last 15 million years (Fig. 5). Of the five ornithorhynchid species identified over the last 63 million years, only one survives today. At the same time, ornithorhynchids have evolved morphologically, transforming from cranially robust, toothed forms in the Miocene to cranially fused skulls lacking adult teeth in extant *O. anatinus*. Although juveniles have rudimentary, poorly formed, rootless molar teeth, these are shed about a month after the young leave the nesting burrow (Griffiths 1978). From a paleontological perspective, lineages that undergo declines over

time of this magnitude in geographic distribution, species diversity, and functional morphology are more likely to suffer extinction than lineages that exhibit increasing geographic distribution, taxonomic diversity, and non-degenerating morphology (Archer et al. 1992).

POPULATION GENETIC STRUCTURE AND DIVERSITY

Molecular clock estimates suggest that the echidna and platypus families diverged from their common ancestor ~17–90 Mya based on different genes and traits, and fossil calibrations (Rowe et al. 2008; Phillips et al. 2009). The oldest estimate suggests this split may have occurred during the mid-Cretaceous (~80–100 Mya—Musser 2003). However, there is no evidence based on fossil biochronology that echidnas even existed as a distinct family prior to about 15 Mya. Mitochondrial DNA (mtDNA—Gongora et al. 2012) and whole-genome data

(Martin et al. 2018) suggest that the emergence of modern platypus populations can be traced back to at least ~0.7–0.8 Mya. Given that *O. agilis* DeVis, which is a junior synonym of *O. anatinus*, is known to have existed in the middle Pliocene at ~3.8 Mya, the possibility cannot be excluded that other events of divergence may have occurred at some point that genetic studies of modern specimens are unable to shed light on.

The phylogeography and population structure of extant platypuses have been investigated using retrotransposon, mtDNA, and microsatellite loci (Akiyama 1998; Warren et al. 2008; Furlan et al. 2010; Gongora et al. 2012; Martin et al. 2018). These studies found that river basins act as discrete population units on the Australian mainland, with greater differences between than within river systems (Gemmell and Westerman 1994; Akiyama 1998; Kolomyjec et al. 2009; Gongora et al. 2012; Furlan et al. 2013). However, there is little genetic differentiation between platypuses on either side of the Great Dividing Range in Victoria (Furlan et al. 2013). Genetic studies also indicate limited gene flow between proximal rivers on the mainland, in contrast to Tasmania where there is less genetic structuring (Kolomyjec et al. 2009, 2013; Furlan et al. 2013).

At the regional level, two divergent evolutionary groups have been identified, one from mainland Australia and the other from Tasmania–King Island (Akiyama 1998; Warren et al. 2008; Furlan et al. 2010; Gongora et al. 2012; Martin et al. 2018). This split may have occurred on mainland Australia before platypuses colonized Tasmania. However, given that platypuses had to be in Tasmania for millions of years as part of the “Gondwanan link” (Lagabrielle et al. 2009), the location of that split is difficult to pinpoint. Furthermore, across the modern range of the platypus, a considerable level of differentiation has been found, with three to four phylogenetic clades based on mtDNA: New South Wales–Victoria, central Queensland, north Queensland, and Tasmania (Gongora et al. 2012). This conclusion is consistent with the number of significant units that have been defined based on microsatellites and whole-genome sequencing (Kolomyjec et al. 2013; Martin et al. 2018).

The recent whole-genome sequencing of 57 platypuses from populations sampled throughout the range of the species confirms a very strong genetic structure in the platypus (*O. anatinus*) over 0.8 Mya, but found no evidence of gene flow between river systems (Martin et al. 2018). In addition, these analyses suggest a historical genetic bottleneck in both north and central Queensland populations. In contrast, individuals from New South Wales appear to have had higher and relatively stable genetic diversity through their history. Furthermore, it was possible to establish the relatedness among 28 of the individuals from the same river system and estimate a de novo mutation rate of 4.1×10^{-9} – 1.2×10^{-8} /bp/generation, considered intermediate for a mammal, lower than humans and chimpanzees but higher than laboratory mice (Martin et al. 2018).

LIFE HISTORY

Morphology.—Platypuses are sexually dimorphic, with males approximately 40% heavier and 15% longer than females (Burrell 1927; Temple-Smith 1973; Furlan et al. 2012; Bino et al. 2015), suggesting that males probably compete for territory, females, and other resources (Brown et al. 2013). There is a clinal increase in size from north Queensland (~700–1,100 g) to Tasmania (1,200–3,000 g—Connolly et al. 1998; Kolomyjec 2010; Gust and Griffiths 2011; Furlan et al. 2012; Bino et al. 2015). However, at finer geographical scales, size variation is confounded by inconsistencies, suggesting involvement of other environmental factors (Kolomyjec 2010; Furlan et al. 2012). The maximum recorded longevity in the wild is 21 and 25 years in captivity (J. Thomas, pers. obs.), although most animals survive approximately 6–15 years (Grant et al. 2004; Serena et al. 2014; Bino et al. 2015).

Temperature regulation.—The pelage consists of an undercoat of dense, short, and finely kinked hairs and an outer layer of spatulate-shaped guard hairs. The underfur retains air during dives, providing efficient insulation against heat loss, which is aided by a counter-current heat exchange in the cardiovascular system supplying the bare extremities (Grant and Dawson 1978). The body temperature of the platypus is maintained close to 32°C in air and water, with an ambient temperature tolerance of 0–30°C (Grant and Dawson 1978; Grant 1983; Grant et al. 1992). Despite sweat glands in the skin, platypuses are not able to withstand environmental temperatures exceeding 30°C (Robinson 1954); its crepuscular and nocturnal activities and burrow use during the day are likely strategies to avoid extreme heat (Grant and Dawson 1978; Bethge et al. 2004).

Senses.—Skin furrows on each side of the head house both the eye and the external ear opening. When submerged these furrows close, as do the nostrils, so that the senses of sight, hearing, and olfaction are absent or reduced (Burrell 1927). The auditory and visual areas of the cerebral cortex are relatively small compared to those receiving neural input from the bill (Bohringer and Rowe 1977). The eyes are small, ~6 mm diameter, with round pupils and flattened corneas characteristic of aquatic vertebrates, perhaps indicating aquatic ancestry. The retina is rod-dominated with some red and blue cones, rhodopsin is the dominant pigment, and there are double cones not found in marsupials or eutherians (Griffiths 1978; Zeiss et al. 2011). Observations of the platypus in the wild suggest acute eyesight, especially sensitive to movement (Burrell 1927). The ear is encased in cartilage rather than bone (Griffiths 1978), there is no external pinna, and no obvious mechanism to conduct water-borne sound to the inner ear (Pettigrew et al. 1998). The cochlea is less sensitive than in other mammals, being most sensitive to frequencies around 4 kHz but responding to frequencies up to 15 kHz (Gates et al. 1974; Krubitzer 1998; Pettigrew et al. 1998).

Platypuses have a pair of cervical scent glands that produce a musky odor and increase in size during the breeding season, suggesting an olfactory role in reproduction (Temple-Smith 1973). Olfaction is unlikely to be important in foraging, as the nares are closed when the platypus is submerged. However, considerable

genetic representation of the vomeronasal system has been identified in the platypus genome (Grus et al. 2007; Keller and Vosshall 2008), possibility indicating this system may be used underwater to detect chemicals produced by prey or other platypuses. A vomeronasal (Jacobson's) organ inside the front of the upper bill opens into the oral cavity (Griffiths 1978).

Specialized sensory structures housed in pores on the skin over the bill and frontal shield are supplied by the trigeminal nerve. Longitudinal rows of these electroreceptors, and uniformly distributed mechanoreceptors, provide electric and tactile senses, presumed to allow platypuses to navigate and locate weak electric fields produced by macroinvertebrate prey species (Scheich et al. 1986; Gregory et al. 1987; Iggo et al. 1992; Manger et al. 1996; Proske et al. 1998; Pettigrew 1999). Although the electric field strengths of common prey species are not within the range detectable by the electroreceptors (Taylor et al. 1992), the signal may be amplified by large numbers of receptors in the bill being stimulated at the same time. Discerning prey direction and location may be achieved by comparing signal strength during side-to-side movements of the bill, along with the input from mechanoreceptors (Pettigrew et al. 1998; Proske and Gregory 2003, 2004).

Diving and diving physiology.—Compared to other mammals, the platypus has a high hematocrit, erythrocyte count, and hemoglobin level, a low mean corpuscular volume, and a high mean corpuscular hemoglobin concentration, which suggests an adaptation to avoid hypoxia during diving (Whittington and Grant 1983; Evans et al. 1994). Platypuses show bradycardia on submersion, from a normal heart rate of 140–230 beats per minute (BPM) to 10–120 BPM. Blood oxygen levels fall rapidly during diving, with rapid restoration of arterial O₂ saturation following dives (Johansen et al. 1966; Evans et al. 1994). Dives have an aerobic limit of 40–59 s (Bethge et al. 2001) and foraging dives in the wild last 30–140 s with around 10–15 s spent on the surface between dives. The frequency of foraging dives is around 75 dives/h (Bethge et al. 2003).

Foraging and energetics.—A pair of cheek pouches lateral to the maxillary and mandibular keratinous grinding pads, which replace the juvenile teeth, store prey items collected underwater for mastication on return to the surface (Griffiths 1978). The digestive tract is relatively short, and its structure is simple (Harrop and Hume 1980). Both the oesophagus and presumptive stomach are small, thin-walled, and lined with non-keratinizing stratified squamous epithelium. Gastric glands and the genes involved in gastric function are absent, and there is therefore no acid secreted and peptic digestion, but Brunner's glands are present at the end of the stomach (Krause 1971). The short small intestine has no villi, but groups of intestinal glands drain into lumina between these numerous surface folds (Krause 1975), and the general structure of the pancreas is similar to other mammals (He et al. 2013). A small caecum (Hill and Rewell 1954) joins the short large intestine, which connects to the rectum, which is of greater diameter than the rest of the tract. Little is known about digestive physiology in platypuses although the diet suggests high proteolytic activity

in the secretions of both the pancreas and the intestinal wall (Harrop and Hume 1980).

Unlike most aquatic mammals, the platypus swims using alternate strokes of its large webbed front limbs, swimming at 0.7–3.6 km/h (Grant and Fanning 2007). Collecting predominantly small organisms on each short dive, foraging normally lasts for 8–16 h per day (Serena 1994; Gust and Handasyde 1995; Otley et al. 2000; Bethge et al. 2003, 2009), although, particularly in winter, animals may forage continuously for more than 30 h per bout (Bethge 2002). When walking, the limbs are splayed away from the body, which is not continuously held above the ground surface, and the energy required for walking is 19–27% higher than for most terrestrial mammals of similar size (Bethge et al. 2001; Fish et al. 2001). The tail is relatively sparsely furred and acts mainly as a fat storage organ (Temple-Smith 1973), containing approximately 40% of the total body fat (Hulbert and Grant 1983), with seasonal changes of body fat occurring during periods of high metabolic demand, especially in winter and during breeding (Temple-Smith 1973; Grant and Carrick 1978; Connolly et al. 2016).

Venom.—Male platypuses are one of few extant venomous mammals (Ligabue-Braun et al. 2012). They have paired venom glands on the dorsocaudal surface of the pelvis, connected via ducts to hollow, keratinous extratarsal spurs on each hind leg; juvenile females have vestigial spur sheaths, lost within the first year of life (Temple-Smith 1973; Grant and Fanning 2007; Williams et al. 2013). The male venom gland may be a derived sweat gland, which enlarges during the breeding season along with increased venom production and male aggressiveness (Temple-Smith 1973). Although the spurs and venom may have had a defensive function in evolutionary history, as hypothesized for Mesozoic mammals (Ligabue-Braun et al. 2012), platypuses currently have few known native predators (Burrell 1927; Grant and Fanning 2007). The venom has a chemically complex composition (de Plater et al. 1995; de Plater 1998; Torres et al. 1999, 2000, 2002b; Torres and Kuchel 2004; Koh et al. 2009) produced by 88 toxin genes (Whittington et al. 2010; Wong et al. 2012). The venom disrupts hemostasis (Martin and Tidswell 1895; Kellaway and Le Messurier 1935), cell membranes (Kourie 1999; Torres et al. 2002a), and nociception (Kourie 1999; de Plater et al. 2001). Venom may have a primarily reproductive function, when males fight each other over access to breeding females, as indicated by cyclic venom production (Temple-Smith 1973; Whittington and Belov 2014) and fresh spur wounds and possible temporary partial paralysis in envenomated males during the breeding season (Fleay 1950; Temple-Smith 1973). Spur wounds heal, indicating that intraspecific envenomation hampers or temporarily disables competitors; death has been recorded only in captive conditions due to multiple spurring (Temple-Smith 1973; Grant and Fanning 2007). The venom causes excruciating local pain in humans that can effectively be reduced using a nerve blocker (Temple-Smith 1973; Fenner et al. 1992). Platypus venom may provide clinically useful substances and improve understanding and treatment of novel pain pathways (Fenner et al. 1992; Whittington and Belov 2014, 2016).

Habitat.—Platypuses are amphibious, inhabiting creeks, rivers, shallow lakes, wetlands, and their riparian margins, in agricultural land, urban areas, and natural environments (Connolly et al. 1998; Goldney 1998; Grant and Temple-Smith 1998a; Otley et al. 2000; Rakick et al. 2001; Munks et al. 2004; Bethge et al. 2009). Mid and lower river reaches in Australia's eastern flowing rivers are generally more favored than upper reaches of rivers (Serena et al. 1998, 2001; Turnbull 1998; Rohweder and Baverstock 1999; Koch et al. 2006; Olsson Herrin 2009; Macgregor et al. 2015). Home ranges vary spatially and temporally with breeding season, age, and sex (Grant et al. 1992; McLeod 1993; Serena 1994; Gust and Handasyde 1995; Serena et al. 1998; Otley et al. 2000; Serena and Williams 2012a; Bino et al. 2018). Preferred habitat tends to include consolidated earth banks with large trees in the riparian zone, vegetation overhanging the stream channel, wide streams with in-stream organic matter, shallow pools, coarse woody debris, and coarse channel substrates, but platypuses still occur in habitats without some of these features, often in quite degraded agricultural settings (Rohweder 1992; Bryant 1993; Ellem et al. 1998; Serena et al. 2001; Milione and Harding 2009). In a Tasmanian study (Lunn 2015), catchment-scale factors (e.g., nearest large stream, catchment area) were found to be more useful indicators of platypus presence in high-order streams, whereas "finer-scale" local habitat variables (e.g., substrate, in-stream barriers) were particularly important indicators of stream use by platypuses in small headwater streams. This result highlights the importance of considering multiple spatial scales in any research into the effect of ecological disturbance on platypuses.

Movement.—Platypuses feed exclusively in the water and rest in burrows, typically in the banks of waterbodies (Grant et al. 1992; McLeod 1993; Serena 1994; Gardner and Serena 1995; Gust and Handasyde 1995; Serena et al. 1998; Otley et al. 2000; Serena et al. 2001); in Tasmania, platypuses are more terrestrial and have been found up to 250 m from water (Otley et al. 2000; Munks et al. 2004). Their activity patterns follow a circadian rhythm, cued by light (Otley 1996; Francis et al. 1999; Bethge et al. 2009). Platypuses are predominantly nocturnal (Grant et al. 1992; McLeod 1993; Gardner and Serena 1995; Francis et al. 1999), although some foraging occurs during daylight, particularly in winter or during lactation (Grant et al. 1992; Grigg et al. 1992; Serena 1994; Gardner and Serena 1995; Gust and Handasyde 1995; Serena et al. 1998; Bino et al. 2018). Individuals may also sometimes align activity patterns with the lunar cycle, synchronizing with moonrise and moonset (Bethge 2002; Bethge et al. 2009). Activity levels also vary throughout the year. In a lake in northern Tasmania, platypuses were most active between late winter and early spring, and least active in mid-summer. Peak activity coincided with the breeding season, mate searching, and increased foraging by lactating females in late spring–summer (Bethge 2002). Interactions between platypuses may also affect temporal partitioning of movements (Hawkins 1998; Bethge et al. 2009). In particular, it has been posited that subordinate individuals may tend to adopt a more variable or fragmented activity pattern or spend relatively more time active during daylight hours (Gust and Handasyde 1995; Hawkins 1998; Bethge et al. 2009).

Most adults appear to maintain reasonably stable home ranges over periods up to several years but these can vary in size between 0.5 and 15 km in linear habitats, with males typically occupying larger home ranges, particularly prior to breeding and as juveniles (Grant and Carrick 1978; Grant et al. 1992; Serena 1994; Gardner and Serena 1995; Gust and Handasyde 1995; Otley 1996; Serena et al. 1998; Bethge 2002; Serena and Williams 2012a; Bino et al. 2018). However, during lactation, females have sometimes been found to forage over larger areas than those used by males (Griffiths et al. 2014). In a subalpine Tasmanian lake, radiotagged individuals occupied areas of 2–58 ha over periods of 22–90 days (Otley et al. 2000). Juvenile males have been found to travel greater distances (Bino et al. 2018) and disperse over 40 km (Serena and Williams 2012a). Although animals typically use only a fraction (e.g., a mean 24–70%) of their home range in a given 24-h period (Serena 1994), adult males and females have, respectively, been documented to travel up to 10.4 km (including backtracking) and 4.0 km overnight (Serena et al. 1998). Platypuses occasionally move overland between water bodies (Taylor et al. 1991; Scott and Grant 1997; Munks and Nicol 2000; Otley et al. 2000) and between river catchments, based on genetic evidence (Kolomyjec et al. 2009; Furlan et al. 2013; Kolomyjec et al. 2013).

Feeding.—The platypus has a distinctive foraging behavior (Bethge 2002) and almost complete reliance on aquatic invertebrates as a food source (Faragher et al. 1979; Grant 1982; McLachlan-Troup et al. 2010). Platypuses forage in both slow-moving pools and faster-moving riffles within streams, and prefer depths of less than 5 m and coarse bottom substrates (Serena et al. 2001; Grant 2004b) that may improve foraging efficiency compared to fine sediment substrates or greater diving depths. Analysis of stomach contents provides little insight into diet and feeding habits of platypuses. Ejection of chitinous parts of macroinvertebrates and crustacean exoskeletons during mastication produces a fine particulate matter that lacks identifiable structures. Most of the useful information on diet has been obtained from analysis of cheek pouch contents. Both sexes feed opportunistically on a similarly wide range of benthic macroinvertebrates of varying sizes (McLachlan-Troup et al. 2010), consuming most invertebrates of a reasonable size, according to availability (Faragher et al. 1979; Grant 1982; McLachlan-Troup et al. 2010; Marchant and Grant 2015). Platypus diets are often dominated by relatively large aquatic macroinvertebrates from the orders Trichoptera, Ephemeroptera, and Odonata (Faragher et al. 1979; Grant 1982; McLachlan-Troup et al. 2010), though small chironomid species may also be important in the diet (McLachlan-Troup et al. 2010; Marchant and Grant 2015; Klamt et al. 2016). Diets including small prey may reflect reduced abundance of preferred larger prey items or increased abundance of smaller items (Marchant and Grant 2015). Platypuses also feed on freshwater crayfish (normally genus *Cherax*) in captivity and on members of this and other genera in the wild, although this is less common (Krueger et al. 1992; Bethge 2002). Daily food consumption is 13–28% of body weight (non-breeding individuals—Krueger et al. 1992;

Munks et al. 2000; Bethge et al. 2001; Thomas et al. 2018b), but is much higher (90–100%) in lactating females (Holland and Jackson 2002), suggesting increased energy expenditure. The platypus can exert top-down influence in aquatic environments, but to a variable extent (McLachlan-Troup 2007). For example, platypuses were found to feed at a low trophic level during drought and on few items in urban environments, indicated by a narrower isotopic niche width as compared to agricultural and forested areas (Klamt 2016). Understanding how these relationships vary temporally and spatially in relation to different environmental conditions, invertebrate biomass, and productivity is still lacking (Marchant and Grant 2015).

Breeding.—Platypuses are seasonal breeders, breeding earlier in lower latitudes (Munks et al. 2000; Temple-Smith and Grant 2001; Grant et al. 2004). In New South Wales, breeding, with the onset of courtship followed by nesting behavior by females, begins around August and continues until young emerge from nesting burrows the following late January to early March. By comparison, in Tasmania, breeding starts 2 months later (Connolly and Obendorf 1998; Munks et al. 2000; Temple-Smith and Grant 2001). Though prey preferences suggest opportunism (see “Feeding” section), the timing of breeding may align with peak food availability during summer months, similar to terrestrial marsupials (Fisher et al. 2013; Lancaster and Downes 2018), but this remains speculative at present. During courtship, female and male platypuses engage in a dance, during which the male holds the tail of the female with his bill, and the female leads them both through a series of slow circles, twists, and turns on the surface of the water, followed by mating (Holland and Jackson 2002; Hawkins and Battaglia 2009; Thomas et al. 2018c). In captivity, reproductive behavior is controlled by the female (Thomas et al. 2018c). Afterwards, female platypuses construct a nesting burrow where they lay one to three eggs ~12–15 mm diameter and ~15–17 mm long (Burrell 1927), which they incubate ~10 days (Griffiths 1978) before the young hatch. Hatchlings are ~15 mm, unfurred, altricial (Manger et al. 1998), and are suckled for 120–140 days based on observations in captivity (Hawkins and Battaglia 2009; Thomas et al. 2018a). Platypus milk contains an antimicrobial protein unique to monotremes, monotreme lactation protein (MLP), which likely evolved to mitigate microbial infection in response to the lack of nipples (Enjapoori et al. 2014) and may perform the functions of other mammalian milk antimicrobials not present in platypus milk (Whittington and Belov 2009).

Nesting burrows are often complex structures with multiple openings, long tunnels (~5 m), a nesting chamber, and “pugs” (sections of burrow backfilled with soil—Burrell 1927). In a large (~0.06 m³), ovoid nesting chamber, the female creates a nest of wet vegetation, mostly grasses, leaves, and bark, dragged into the burrow with her tail (Holland and Jackson 2002; Thomas et al. 2018a). Two nest-like mounds had a dry recess, along a stream cave in Tasmania, which was made of fibrous roots and small amounts of leaf material and branchlets of moss (Munks et al. 2004). The burrow and its collected vegetation provide security and suitable microclimate conditions

for incubation and hatching of the eggs and development of the young. Newly emerged juvenile platypuses are 65–70% of their adult mass and 83–87% of their adult length (Grant and Temple-Smith 1998b). In captivity, juveniles are weaned within days of emergence and feed on available aquatic invertebrates similar to adults (Thomas et al. 2018c). Dispersal of juveniles remains poorly known, except for two studied populations where 78% of females and 94% of males (Bino et al. 2015), and 75% of females and 88% of males (Serena et al. 2014) were not recaptured after their first year, suggesting high dispersal or mortality (Bino et al. 2015).

THREATS

Historical accounts of past numbers of the platypus resemble those of many other previously common species that have subsequently declined (Gaston 2011). Globally, there is growing concern that extinction risk to common and widespread species is rapidly increasing, with little analysis or implementation of conservation assessment and actions. Conserving only the formally designated threatened species, while neglecting all other native fauna, hinders and even undermines biodiversity conservation, as is the case for the platypus (Lunney 2017a, 2017b). Platypus populations are at risk of declines and local extinctions because of the many and synergistic threats to their survival, compounded by our current lack of information, particularly of population dynamics and the impacts of anthropogenic activities (Lunney et al. 2008; Woinarski et al. 2014). Impacts of threatening processes and evidence of declines across the species’ entire range rely almost entirely on two long-term studies of densities, reproduction, age structure, and survival (Grant 2004a; Serena et al. 2014). Quantifying the effects of threatening processes and their impacts on population viability is very difficult for a species like the platypus, remaining a key knowledge gap essential for developing rigorous risk assessments that can guide effective conservation actions (Mace et al. 2008).

The drivers of declining distribution and population size for the platypus are many, widespread, and synergistic. Distribution of the platypus coincides with major threatening processes (Kingsford et al. 2009), including highly regulated and disrupted rivers (Kingsford 2000; Grant and Fanning 2007), extensive riparian and lotic habitat degradation by agriculture and urbanization (Grant and Temple-Smith 2003), and fragmentation by dams and other in-stream structures (Kolomyjec 2010; Furlan et al. 2013). By-catch mortality in fishing gear (Grant and Fanning 2007; Serena and Williams 2010a), diseases, and predation by invasive foxes and feral dogs (Serena 1994; Connolly and Obendorf 1998; Grant and Fanning 2007) also impact platypus populations.

Projected climate change will likely affect platypus distribution and numbers, even though platypuses occupy a broad environmental gradient. Projected decreased precipitation and increased evapotranspiration have significant implications for habitat availability by reducing thermally suitable habitat (Klamt et al. 2011). Current projections predict both drought frequencies and severity are likely to increase (CSIRO and

Bureau of Meteorology 2015), further threatening small and isolated populations. Extended droughts can dry up creeks, likely reducing the extent of critical refugia, forcing platypuses to move overland where risk of predation is high, and exacerbating competition within decreasing numbers of pools.

Past fur trade and hunting.—Platypuses were hunted for the fur trade in the late 19th and early 20th century, driven by ongoing demand and high commercial prices for platypus skins, until nation-wide protection by 1912. A single rug or garment needed more than 50 platypus skins (75 platypus skins were used for a rug on display at the Australian Museum), making their skins more valuable than any other Australian animal (Goulburn Herald 1905). Skins were common in the Sydney market, with 754–2,356 sold annually between 1891 and 1899 (Sydney Wool and Produce Journal and Sydney Wool and Stock Journal). Some were also exported to London, although many more were undoubtedly smuggled, disguised as other small mammal skins (Burrell 1927). One furrier reported selling single-handedly over 29,000 skins before World War I (The Nowra Leader 1938). Sportsmen also shot hundreds of platypuses (The Don Dorrigio Gazette and Guy Fawkes Advocate 1919), some making a living from this activity (Grant and Denny 1991). One person shot many thousands over 32 years work (Grant and Fanning 2007). Given records of skin sales account for 10–100% of current population estimates (30,000–300,000—Woinarski and Burbidge 2016) and the slow reproductive rate of platypuses (1.5 young per year, with only half of females breeding in a given year—Bino et al. 2015), the impacts of the fur trade were probably never reversed, leaving many populations vulnerable to the many increasing threatening processes.

Habitat destruction.—Widespread land clearing and degradation of ecological function (disruption of water, nutrient, mineral, and carbon cycles) are major present-day drivers of declines and local extinctions of platypuses. Platypuses require stable banks of rivers and creeks to build burrows for resting and breeding purposes (Serena et al. 2001). Clearing, grazing, and watering access by livestock have severely degraded river banks and riparian vegetation (Lunney et al. 2004), increasing sedimentation, which in turn smothers stream beds and further degrades foraging habitat (Klamt 2016). Catchment-scale modification is also a significant threat, impacting food availability (Magierowski et al. 2012) and restricting overland movements. Degraded landscapes can overheat and dry out rapidly due to the loss of soil carbon, reducing habitat size and destroying drought refugia (Bauer and Goldney 1999; Kerle et al. 2014). In turn, runoff has increased dramatically, adding to soil loss and in-channel sedimentation (Walker et al. 1993; Minella et al. 2018).

Water resource development, including the building of dams, extraction of water, and development of floodplains, has caused widespread degradation of freshwater habitats within the platypus' range (Kingsford 2000; Grant and Fanning 2007). River regulation alters the natural flow regime including both magnitude and frequency of flow events, degrading the ecological health of impacted river sections (Gilligan and Williams 2008). This process includes channel habitat destruction, accumulation

of fine sediment (Coleman and Williams 2017), and encroachment of terrestrial vegetation into river channels. Altering the natural flow regime can impact resources required by platypuses, as well as reproduction (Serena and Grant 2017).

Hydrologic connectivity critically maintains the ecological integrity of river systems, mediating transfer of organic and non-organic matter, energy, as well as organisms (Pringle 2003). Platypuses make extensive movements that are almost certainly affected by the many weirs and large dams (Bino et al. 2016) that impede connectivity between populations. Dams are significant physical barriers (e.g., Dartmouth Dam on the Mitta Mitta River in the state of Victoria is 120 m in height) but also potentially ecological barriers, given the significant sizes of dam reservoirs (e.g., Dartmouth Dam reservoir, ~33 km long) and their limited food resources for platypuses, given their depth. Loss of connectivity between populations restricts source-sink dynamics (Hanski 1999) in cases of localized extinction as well as reducing genetic viability, adversely impacting conservation outcomes (Frankham et al. 2017).

Although platypuses still occur in urban and peri-urban environments, declines and localized extinctions in the most heavily urbanized areas indicate platypuses are sensitive to urbanization (Grant 1992; Grant 1998; Lintermans 1998; Serena et al. 2014). Throughout Melbourne, platypus distribution has been found to be limited by catchment imperviousness (Serena and Pettigrove 2005; Martin et al. 2014), indicating platypuses are impacted by the altered flow regimes of urban streams. Urban streams typically suffer from high flow variability, with increased magnitude and frequency of high flows, and reduced and extended baseflows (Walsh et al. 2005, 2012). High flow events may increase foraging energetics for platypuses (Gust and Handasyde 1995); summer flood events can reduce recruitment (Serena et al. 2014; Bino et al. 2015; Serena and Grant 2017), and decreased baseflow during drought lowers overall habitat availability for platypuses and their prey (Marchant and Grant 2015), also increasing predation risk and reducing longitudinal connectivity and fragmenting populations. Urbanization is also associated with increased water pollution, increased risks of predation, litter entanglement, road kill, and greater disturbance from human activities (Connolly et al. 1998; Serena and Williams 1998, 2010a).

Fishing by-catch.—From the late 1880s, a commercial fishery extended over much of the Murray-Darling Basin, especially in the middle and lower reaches of the Murray and Murrumbidgee Rivers (Grant 1993). Use of small mesh net sizes almost certainly impacted platypus numbers in these rivers, until larger mesh was introduced from the mid-1900s to reduce the capture of larger breeding fish. Following the introduction of trout species, the use of nets or traps in headwater streams was banned in New South Wales in 1902, providing some protection to platypuses in these regions (Grant 1993). In Victoria, where mortality was tracked and could be assigned, 56% of 186 platypus mortalities (1980–2009) were caused by drowning in illegal nets or enclosed traps (also referred to as opera house traps) set to capture fish or crustaceans (Serena and Williams 2010a). Such enclosed traps, which are left unattended in the water for

extended periods, have relatively small openings (7.5–10 cm diameter) at the ends of internal funnels to prevent animals from escaping. Platypuses enter these traps either by accident or because they are attracted to trapped prey. Consequently, Victorian Fisheries Authority announced a state-wide ban on use of enclosed traps from 2019 (VFA 2018).

Invasive and feral species.—During overland movements, such as juvenile dispersal or searching for refugia during dry periods, platypuses are particularly vulnerable to predation by invasive terrestrial carnivores: red foxes (*Vulpes vulpes*), feral dogs (*Canis familiaris*), and feral house cats (*Felis catus*—Grant and Fanning 2007), as well as by native Tasmanian devils (*Sarcophilus harrisii*) in Tasmania. In the mid-1990s in Tasmania, 40% of platypus deaths were due to attacks by domestic dogs (Connolly et al. 1998), based on necropsies of 25 carcasses. In Victoria, predation by raptors, dogs, or foxes accounted for 13% ($n = 24$) of documented platypus deaths (Serena and Williams 2010a). Interactions with European carp (*Cyprinus carpio*) remain unknown, although there are likely indirect effects such as increased sedimentation and reduced benthic food availability (Serena and Williams 2010b).

Pollution.—Platypuses can get stuck in in-stream structures, such as pipes or hydroelectric turbines (Serena and Williams 2010a). Platypuses are incapable of using their highly specialized front feet to remove litter wedged around their body, which ultimately causes deep lesions. They frequently get entangled in discarded hooks and loops of fishing line (Serena and Williams 2010a). Plastic or rubber loops (e.g., canning jar rings, engine gaskets, cable-ties, tamper-proof seals from plastic-lidded food jars, child's plastic bracelets, hair bands) have been recovered from the neck or torso of up to nearly 40% of animals captured in some suburban streams near Melbourne (Serena and Williams 1998, 2010a).

Disease.—Many infectious agents have been isolated from platypuses but relatively few cause serious disease (Whittington et al. 1992; Booth and Connolly 2008; Supplementary Data SD1). The exception is mucormycosis caused by *Mucor amphibiorum*, an environmental fungus first detected in platypuses in 1982, which causes a lethal infection in Tasmanian platypuses and is a considerable threat to mainland platypus populations if introduced (Munday and Peel 1983; Gust et al. 2009; Gust and Griffiths 2011). Mucormycosis causes a severe granulomatous and often ulcerative dermatitis, sometimes progressing to underlying tissues or disseminating to the lungs (Connolly 2009). Death may also result from secondary bacterial infections or impaired thermoregulation and mobility. Diagnosis is based on culturing the dimorphic fungus from platypus lesions, supported by morphological, molecular, or serological tests, such as an ELISA (Whittington et al. 2002; Connolly et al. 2010). Mucormycosis may also be detectable clinically or via signs or presence of spherules in cytology or histology of lesions, but this is less accurate than culture. *Corynebacterium ulcerans* or non-*Mucor* fungal skin disease can cause similar infections and cutaneous foreign body reactions (Connolly et al. 1998; Macgregor et al. 2017b). Mucormycosis was accidentally introduced to toads and frogs

on the Australian mainland (Northern Territory, Queensland, New South Wales) by captive frogs from Melbourne and Perth, but the infection has not been recorded in mainland platypuses. Isolates of *M. amphibiorum* are susceptible to Amphotericin B and some disinfectants, with some hope of future vaccine development (Connolly et al. 1998; Connolly 2009; Webb et al. 2012).

An adenovirus-like virus causes a cytomegalic inclusion renal disease (Whittington et al. 1990) and a putative papilloma virus causes webbing papules (Booth and Connolly 2008). Between 47% and 66% of platypuses in New South Wales and 10% in Tasmania had leptospirosis based on serology, while in Victoria, 25% of platypus necropsied showed suggestive nephritis histologically (McColl and Whittington 1985; Loewenstein et al. 2008; Macgregor et al. 2017b). The *Ixodes ornithorhynchi* tick is common and may cause a mild dermatitis but importantly, it can be a vector of the hemoparasites *Theileria ornithorhynchi* and *Trypanosoma binneyi* (Booth and Connolly 2008), with the former sometimes causing hemolytic anemia in immunocompromised platypuses (Kessell et al. 2014).

CONSERVATION AND RESEARCH PRIORITIES

Effective conservation of platypus populations hinges on controlling threatening processes, supported by investment in systematic long-term monitoring of trends in population sizes, demographics, distribution, genetics, and diseases. These priorities are particularly important in small streams, where populations are small and permanent drought refugia may not persist as they do in larger streams. Our understanding of how threatening processes impact individual health, population dynamics (e.g., survival, dispersal), and habitat quality remains largely qualitative in nature, demanding we develop quantitative models that allow predicting population viabilities, critical for prioritizing conservation management strategies. Whether dams and roads impede connectivity between platypus populations remains unevaluated, potentially affecting genetic diversity and severely degrading adaptive potential (Holderegger and Wagner 2006; Frankham et al. 2017). Synergistic impacts of habitat destruction and barriers, along with forecasted increasing frequency and intensity of droughts due to climate change that will reduce thermally suitable habitat (Klamt et al. 2011), will further jeopardize genetic and population viability in fragmented and isolated populations (Martin et al. 2018). Delineating the thermal tolerance of the species is needed to better predict the impacts of increasing temperatures (Kearney and Porter 2009). Use of novel genetic technologies (e.g., genomics, transcriptomics, proteomics, metabolomics, metagenomics, and epigenomics) can offer significant insights into many aspects of life history as well as the capacity of platypuses to adapt in response to changing climates and diseases (Amato et al. 2009).

Reducing the extent and intensity of identified threats is required to increase the likelihood of long-term survival of platypuses across eastern Australia. Restoration of riparian habitat through rehabilitation of river banks by replanting trees and restricting livestock access should become a priority. Improving water quality

and restoration of natural flow regimes could improve functioning and food-web structures, while maintaining longitudinal connectivity and drought refugia. Environmental flows (i.e., dedicated flows) could also be used as a management action to ensure that these refugia do not dry out. Connectivity between populations must also be assessed and maintained by limiting and removing in-stream barriers (e.g., weirs, dams, roads) wherever possible and potentially developing “platypus-ways” across barriers, which require dedicated design planning and research. Considerable uncertainty remains regarding the dispersal behavior of juveniles both in terms of timing and distances, critical knowledge gaps for understanding metapopulation dynamics. Platypuses need to be protected from invasive predators when they move overland during dry periods or when dispersing. There should be a nation-wide ban of closed traps targeting crustaceans or fish in freshwater habitats, along with reduction in pollution to reduce mortality. Zoos play an important role in platypus conservation by conducting research, contributing to better public awareness of threatening processes, and establishing insurance populations to secure genetic diversity, particularly when considering potential impacts of climate change and the increased likelihood of severe droughts. Success of captive breeding remains sporadic with only four females breeding in zoos to date (J. Thomas, pers. obs.; J. O’Brien, Taronga Zoo, pers. comm., 2018), suggesting more directed efforts are needed to understand breeding requirements, including habitat and mate selection.

Given increasing support for research on charismatic species (Lunney 2012), the iconic platypus can be a focus for citizen science wildlife surveys that can improve knowledge of distribution as well as establish baselines for long-term monitoring (Grant and Llewellyn 1992; Lunney et al. 1998, 2004; Turnbull 1998; Grant et al. 2000; Otley 2001). Relying on sightings in the form of citizen science or community-based surveys requires scrutiny, such as concurrent systematic surveys (Lunney et al. 2004) to establish a reliable estimate of detection biases and how these can inform on population densities. We conclude that conserving the platypus, an Australian icon and an evolutionarily unique animal (Isaac et al. 2007), must become a priority at all levels of government and for the public through increased community awareness of threats. An appropriate level of listing for the platypus on State and Federal threatened species schedules (e.g., Environment Protection and Biodiversity Conservation Act 1999) is also needed based on improved understanding of distributional patterns and demographic processes, focused research, and management of the many threats raised in this review.

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SUPPLEMENTARY DATA

Supplementary Data SD1.—Infectious disease agents of the platypus.

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