

Wildlife parasitology in Australia: past, present and future

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Abstract. Wildlife parasitology is a highly diverse area of research encompassing many fields including taxonomy, ecology, pathology and epidemiology, and with participants from extremely disparate scientific fields. In addition, the organisms studied are highly dissimilar, ranging from platyhelminths, nematodes and acanthocephalans to insects, arachnids, crustaceans and protists. This review of the parasites of wildlife in Australia highlights the advances made to date, focussing on the work, interests and major findings of researchers over the years and identifies current significant gaps that exist in our understanding. The review is divided into three sections covering protist, helminth and arthropod parasites. The challenge to document the diversity of parasites in Australia continues at a traditional level but the advent of molecular methods has heightened the significance of this issue. Modern methods are providing an avenue for major advances in documenting and restructuring the phylogeny of protistan parasites in particular, while facilitating the recognition of species complexes in helminth taxa previously defined by traditional morphological methods. The life cycles, ecology and general biology of most parasites of wildlife in Australia are extremely poorly understood. While the phylogenetic origins of the Australian vertebrate fauna are complex, so too are the likely origins of their parasites, which do not necessarily mirror those of their hosts. This aspect of parasite evolution is a continuing area for research in the case of helminths, but remains to be addressed for many other parasitic groups.

Additional keywords: acanthocephalans, arthropods, molecular methods, morphology, nematodes, platyhelminths, protists.

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Introduction

In 1909, T. H. Johnston and J. B. Cleland, working at The Bureau of Microbiology in Sydney set out to ‘document the parasites of Australia’s native fauna’ (Johnston and Cleland 1909), probably not aware of how enormous that task would be. Johnston, first at the University of Queensland and subsequently at the University of Adelaide, spent the rest of his life fulfilling this laudable aim both through his own work and those of the many students he taught and inspired. As a consequence of his influence, the Queensland Institute of Medical Research and the Queensland Department of Primary Industry engaged in wildlife parasitology to some degree over many years, joined later by the University of Queensland’s Department of Parasitology. Independently, the CSIRO Division of Wildlife Research became involved in wildlife parasitology, initially with regard to the control of pest species, but subsequently with the indigenous mammalian fauna. Consequently, this undertaking has continued over many decades. The history of these developments has been described in Beveridge and O’Donoghue (2009).

The impetus for the study of parasites of wildlife has come from several sources, intellectual curiosity being a predominant

one. In decades past, there was also considerable interest in the helminth parasites of marsupials that could be transmitted to and from livestock such as the common liver fluke (*Fasciola hepatica*) (Spratt and Presidente 1981) or the hydatid tapeworm (*Echinococcus granulosus*) (Durie and Riek 1952) as well as the endemic tick species that caused paralysis in livestock and domestic animals (*Ixodes holocyclus*) (Clunies-Ross 1924). In addition, bacterial diseases such as Q fever, which affects humans and domestic animals, but also has reservoirs in wildlife and could be transmitted by ticks (Derrick 1944), became foci of research for wildlife parasitology. More recently, the desire to document the extent of biodiversity within Australia, led by the Australian Biological Resources Study, has included parasites (Just 1998) and has significantly aided taxonomic work in this area.

The realisation that some parasites (helminths, protists and arthropods) can cause significant disease and animal welfare issues in wildlife has been an additional impetus to study parasites of wildlife (Arundel *et al.* 1977). Finally, ecological studies of parasites of wildlife, whether they be life-cycle studies (e.g. Spratt and Haycock 1988) or community ecology of helminths (e.g. Spratt 1987) or the natural distributions of ticks

(e.g. Bull *et al.* 1989) have made contributions to ecological studies generally in Australia.

At the same time, it has to be remarked that the advances that have been made have received relatively little funding as the area falls between the remits of various government departments and is usually of no or little pecuniary interest.

The following review is intended to highlight both the advances made to date focussing on the work, interests and major findings of researchers over the years and then to identify the current significant gaps that exist in our understanding of parasites of wildlife in Australia. Due to the diversity of parasites and researchers involved, it is difficult to cover this very broad topic in a consistent fashion. Protists and arthropods are more easily dealt with by considering parasitic taxonomic groupings (piroplasms, kinetoplastids, apicomplexans for the protists and lice, fleas ticks and mites for the arthropods) as these taxa tend to occur across major classes of vertebrates, while the helminths, which often show a greater degree of specificity at this level can be dealt with more concisely by considering the host groups (mammals, birds, reptiles and amphibians). The review is therefore divided into three sections covering protist, helminth and arthropod parasites.

Protists

A major review of the parasitic protists known in Australia by O'Donoghue and Adlard (2000) provides a convenient overview of the discipline. Recent surprising findings in the genera *Hepatozoon* (Šlapeta *et al.* 2017) and *Cryptosporidium* (Thompson *et al.* 2016) subjected to modern molecular technologies highlight both a new understanding of species limits and of phylogenies within the parasitic protists. As an example of what lies ahead for exploration in wildlife, a recent survey of 711 ticks removed from dogs (498), cats (139) and horses (74) throughout Australia were screened for piroplasms and *Hepatozoon* spp. using conventional PCR and Sanger sequencing (Greay *et al.* 2018). In addition to *Babesia canis vogeli* and *Theileria orientalis* (genotype Ikeda), already known in the country, the exotic tick-borne *Hepatozoon canis* was identified along with eight novel piroplasms, a species of *Hepatozoon* and a novel species of Sarcocystidae. Eight new taxa representing the genera *Babesia* (2), *Hepatozoon* (2) and *Theileria* (4) were described, implying just how little we know about the protists, even those occurring in our companion and domestic animals.

Piroplasmida

Babesia

Species of *Babesia* occur in a wide range of domestic and wild mammals, *B. bigemina* and *B. bovis* in cattle representing the most economically important and pathogenic species in Australia (Dawood *et al.* 2013). Although several species of *Babesia* have been described or identified in dasyurid, peramelid, potoroid and macropodid marsupials as well as the echidna, reports of clinical babesiosis in wildlife have been rare (Backhouse and Bolliger 1959; Mackerras 1959; Barker *et al.* 1978; O'Donoghue and Adlard 2000; Paparini *et al.* 2012; Dawood *et al.* 2013; Donahoe *et al.* 2015b). Disease is associated with infections in male antechinus with physiological stress in the postmating period (Cheal *et al.* 1976; Barker *et al.* 1978) and has been reported in

eastern grey kangaroos with neurological signs, depression and anaemia attributed to stress due to handling, transportation and captivity (Dawood *et al.* 2013).

Babesia macropi infection was considered the primary cause of anaemia, lethargy and neurological signs resulting in morbidity and death in 38 hand-reared and free-ranging juvenile eastern grey kangaroos and three agile wallabies (Donahoe *et al.* 2015b). The first case of human babesiosis thought to be locally acquired was reported recently (Senanayake *et al.* 2012). Further research on species of *Babesia* in wildlife are required, first and foremost to develop sensitive diagnostic tests for detection of infection in live animals and molecular studies to determine host specificity, vectors and reservoir hosts.

Theileria

Three species of *Theileria* have been described based on morphological data, one each from the echidna and platypus and *T. peramelis* from the southern brown and long-nosed bandicoots and the long-nosed potoroo (Priestley 1915; Mackerras 1959; Collins *et al.* 1986). In addition, four species have been described from macropodids and potoroids based on morphological and molecular data (Clark and Spencer 2007; Lee *et al.* 2009; Paparini *et al.* 2012, 2015). The genetic distance of 3.4% between *T. gilberti* and two *T. brachyuri* isolates of Clark and Spencer (2007) indicates that the two isolates represent two genetically distinct species (Lee *et al.* 2009). On the other hand, a 0.2% genetic distance between *T. penicillata* of Clark and Spencer (2007) and an isolate from the long-nosed potoroo indicates that the latter isolate is conspecific with *P. penicillata* (Lee *et al.* 2009).

Only one study has described the sporadic presence of tetrads and putative extraschizont stages, the distinguishing features of the genus *Theileria* (Paparini *et al.* 2015). DNA sequences of *T. ornithorhynchi* obtained from platypus blood and ticks formed a novel monophyletic group, basal to most known piroplasm clades, reflecting the ancestral position of the clade from an ancient mammalian lineage of host (Paparini *et al.* 2015). Incomplete sampling, morphology-based classification and ambiguous microscopic identifications highlight the current inadequacies of the molecular systematics for the Piroplasmida.

Kinetoplastida

Trypanosoma

Thompson *et al.* (2014a) recently reviewed the diversity and distribution of trypanosomes of Australian mammals. Trypanosomes are known also from reptiles and amphibians (Mackerras 1961; Jakes *et al.* 2003), birds (Mackerras and Mackerras 1960), and frogs and fish (Mackerras and Mackerras 1961). The early studies were based on traditional morphological methods but in recent years, culturing and molecular methods have offered more sensitive identification techniques as well as rapid screening of multiple blood samples (Noyes *et al.* 1999; Hamilton *et al.* 2004, 2005). As a consequence, there has been a recent surge in studies on trypanosomes occurring in wildlife with eight molecularly determined species and additional incompletely identified species infecting platypus, a wide range of marsupial species and native rats and mice (Averis *et al.* 2009;

McInnes *et al.* 2009). Evidence includes mixed infections (McInnes *et al.* 2011a, 2011b; Thompson *et al.* 2013; Godfrey *et al.* 2018) multiple host species (Austen *et al.* 2009, 2015; McInnes *et al.* 2011a, 2011b), novel genotypes (Austen *et al.* 2009, 2015, 2016; Paparini *et al.* 2014), morphological polymorphism (Thompson *et al.* 2013) and potential pathogenesis in endangered species (McInnes *et al.* 2011a, 2011b; Thompson *et al.* 2013, 2014a, 2014b; Austen *et al.* 2015; Godfrey *et al.* 2018). Although no life cycles are known, molecular detection of trypanosomes in an aquatic leech suggest that these may be vectors for *T. binneyi* and related genotypes (Paparini *et al.* 2014). Experimental infection of the agile wallaby (*Notamacropus agilis*) and the dusky pademelon (*Thylogale brunii*) with *T. evansi* in Papua New Guinea, where it is endemic, resulted in high levels of parasitaemia, morbidity and mortality (Reid *et al.* 2001). Given the diversity of tabanid fly intermediate hosts in northern Australia, and their preponderance for feeding on horses, kangaroos and pigs, this indicates a clear biosecurity concern should *T. evansi* become established in Australia (Muzari *et al.* 2010).

Two distinct clades of trypanosomes have been recognised, one of mammalian trypanosomes of African origin, the other specific to Old and New World bats, mammalian species in Central and South America and a species from a kangaroo (Stevens *et al.* 1999). The first implies an evolutionary history confined to Africa, the latter an evolutionary history confined to an ancient southern supercontinent, possibly in marsupials. Palaeogeographical evidence places the time of divergence of the two clades in the mid-Cretaceous following the break up of Gondwana and the separation of Africa, South America and Euramerica.

Delvinquier and Freeland (1989) examined 924 anurans representing 62 species from five mainland States and the Northern Territory for blood trypanosomes. They summarised current knowledge and described, but did not name, six additional species, all from Queensland.

Given the fascinating information about species of *Trypanosoma* in mammals, mainly in Western Australia, similar investigations of species occurring in mammalian, avian and reptilian wildlife, particularly in eastern Australia, remains an ongoing challenge.

Leishmania

Australia has long been considered free of endemic species of *Leishmania* and of suitable phlebotomine (sandfly) vectors for its transmission. However, Rose *et al.* (2004) reported cutaneous leishmaniasis in a red kangaroo in the Northern Territory and subsequent infections have been reported in northern and black wallaroos and agile wallabies (Dougall *et al.* 2009). A day-feeding ceratopogonid midge, *Forcipomyia (Lasiohelea)* sp. 1, is the biological vector (Dougall *et al.* 2011). This represents the first evidence of a vector of a species of *Leishmania* other than phlebotomine sandflies anywhere in the world and raises future biosecurity concerns that this or a similar midge species may be potential vectors for human pathogenic species should they enter the country. The species was formally described as *Leishmania (Mundinia) macropodum* (Barratt *et al.* 2017). Subsequently, insect trapping in an area recommended by Dougall *et al.* (2011) resulted in the discovery of a novel trypanosomatid, *Zelonina*

australiensis, isolated from the blackfly *Simulium (Morops) dycei* (Barratt *et al.* 2017).

Opalinida

Zelliriella and Protoopalina

Delvinquier (1987) reviewed the literature on the Opalinidae occurring in Australian anurans, a group of specialised flagellate protists living in the rectum of frogs and toads. Prior to this, Tate (1963) had completed the first life cycle of an Australian opalinid, *Zelliriella binucleata*, occurring in *Lymnodynastes tasmaniensis*. He noted that *Z. binucleata* passes through a *Protoopalina* stage in its life cycle, both in the tadpole and in the frog. Several previously described species of *Protoopalina* have been found to be stages in the life cycle of *Z. binucleata*, hence there is an imperative for complete life-history descriptions when making a taxonomic study of any member of the group. Ultrastructural studies of *Protoopalina australis*, occurring in several bufonid, hylid and myobatrachid anuran amphibians, indicated that microfibrillar tracks and regular arrays of cortical vesicles which occur in the multinucleate genera *Opalina* and *Cepedea*, were absent from the binucleate genera (Patterson and Delvinquier 1990). This observation and the discovery of a new genus, *Protozelliriella*, prompted these authors to review understanding of the evolution of slopalines in favour of a common origin for the multinucleate genera *Opalina* and *Cepedea* (Patterson and Delvinquier 1990). They concluded that the evolution of the slopaline genera was substantially complete after the break up of the supercontinent Gondwana between the Triassic and the Cretaceous periods.

Apicomplexa

Haemogregarina

Numerous species of *Haemogregarina* have been described from Australian reptiles and *H. hylae* from the green tree frog (*Litoria caerulea*) (O'Donoghue and Adlard 2000). One in particular, *Hemolivia mariae*, is found in the erythrocytes of a natural population of the sleepy lizard, *Tiliqua rugosa*, in South Australia and is transmitted by two tick species, *Amblyomma limbatum* and *Bothriocroton* (formerly *Aponomma*) *hydrosauri* (Smallridge and Paperna 1997; Smallridge and Bull 1999, 2000). Tick loads on infected and uninfected free-ranging lizards are not significantly different and there is no evidence for infection-induced mortality in ticks (Smallridge and Bull 2001). Bouma *et al.* (2007) demonstrated that lizards have smaller home ranges when infected with *H. mariae* than when no infection is detected. However, lizards with larger home ranges were more susceptible to infection under experimental exposure to *H. mariae*, possibly sacrificing defence against pathogens by increased activity associated with maintaining home ranges and mating opportunities, consequently gaining higher parasite loads which in turn inhibit their activity.

Hepatozoon

Early work on the blood parasites in Australian vertebrates undertaken by M. J. and I. M. Mackerras stands out as a landmark in the field (Mackerras 1959, 1961; Mackerras and

Mackerras 1960, 1961). M. J. Mackerras (1959) demonstrated that the mite, *Laelaps echidninus*, was the vector of *Hepatozoon muris* occurring in native and introduced murid rodents, infection occurring during grooming when rodents eat the mites. Recently, an intraerythrocytic parasite found in the blood of a yellow-bellied glider (*Petaurus australis*) from Queensland was tentatively classified as *Hepatozoon* based on tissue site and morphological features (Zhu *et al.* 2009). However, molecular techniques using SSU and LSU rDNA and comparison with available sequences from mammalian and non-mammalian blood parasites revealed that it was most closely related to cyst-forming coccidia such as the genera *Toxoplasma*, *Neospora*, *Hammondia* and *Besnoitia*. Until life cycles have been determined it is not known if this coccidian represents *Hepatozoon petauri* described by Welsh and Barling (1910) and reported also by Mackerras (1959) and Bettiol *et al.* (1996).

Using next-generation DNA sequencing, Šlapeta *et al.* (2017) demonstrated that the presence of *Eimeria echidnae* DNA in the blood of echidnas was associated with atoxoplasma-like stages in white blood cells, suggesting that *Hepatozoon tachyglossi* blood stages are disseminated stages of *E. echidnae*. The development of molecular technologies for the detection of these organisms has significant implications for the true identity of the seven named species of *Hepatozoon* from mammals and the single named species from a reptile listed by O'Donoghue and Adlard (2000). This area of investigation is ripe for further significant advances employing molecular techniques.

Klossiella

Species of *Klossiella* are the aetiological agents of renal coccidiosis in Australian macropodids, possums, gliders and murids but are considered to be only mildly pathogenic in normally healthy animals (Barker *et al.* 1975, 1984; Bennett *et al.* 2007).

Eimeriida

Cryptosporidium and *Giardia*

Both the flagellate genus *Giardia* and the facultative epicellular apicomplexan genus *Cryptosporidium* are causative agents of enteric disease and are of enormous significance in domestic animal and human health. Both are most frequently water-transmitted in spite of their taxonomic associations.

Thompson *et al.* (2016) provided an historical review of *Cryptosporidium* and the revelations that have resulted in the phylogenetic reclassification of the genus from a coccidian to a gregarine. *Cryptosporidium* 'marsupial genotypes' have been identified in 12 marsupial species, seven of which belong to the Macropodidae (kangaroos and wallabies) (Power 2010). In addition to the marsupial-specific *C. fayeri* and *C. macropodum*, western grey kangaroos may be infected with a wider range of *Cryptosporidium* species and genotypes, including livestock species such as *C. xiaoi* (Yang *et al.* 2011). Novel genotypes of *Cryptosporidium* have been identified in captive and wild Tasmanian devils (Wait *et al.* 2017). However, their extent in the endemic fauna and their zoonotic significance remain uncertain. Common quails (*Coturnix coturnix*), mallard ducks (*Anas platyrhynchos*), ring-necked pheasants (*Phasianus colchicus*)

and a budgerigar (*Melopsittacus undulatus*) infected with *Cryptosporidium* sp. exhibited clinical signs of respiratory distress (O'Donoghue *et al.* 1987b). In repeated cross-transmission studies, oocysts from quail and pheasant were infective to chickens, but not to mice.

Infection of humans in Tasmania with *Giardia* spp. is often referred to as 'bushwalkers diarrhoea' and thought to be associated in part with the high prevalence of infection in numerous marsupial species, especially bandicoots (*Isodon obesulus*) (Bettiol *et al.* 1997; Kettlewell *et al.* 1998). In contrast, a low prevalence of infection was reported in a large sample of many wildlife species from different geographic areas in Western Australia (Thompson *et al.* 2010). Highest prevalence was again in bandicoots (*Isodon obesulus*), more than half harbouring the host-specific 'quenda' genotype, *Giardia peramelis* (Adams *et al.* 2004; Hillman *et al.* 2016b). Zoonotic forms of *Giardia duodenalis* were the only other species found, implying that native mammals in Western Australia, with the exception of the quenda, do not harbour distinct strains of *Giardia*, as occurs in Tasmania. Novel genotypes of *Giardia* have been identified in captive and wild Tasmanian devils (Wait *et al.* 2017). The occurrence of zoonotic genotypes in marsupials in the four southern states implies transmission routes between humans and wildlife and vice versa (Thompson *et al.* 2008; Vermeulen *et al.* 2015; Wait *et al.* 2017).

Eastern and western grey kangaroos are the most abundant marsupial species inhabiting watersheds in eastern and western Australia but to date there have been no reports of outbreaks of *Cryptosporidium* or *Giardia* due to drinking this water nor have marsupial-derived genotypes been identified in humans (Power *et al.* 2005).

Young birds appear most susceptible to *Giardia* infection, with highest mortality rates in psittacines although other causative factors may be involved (Ladds 2009). *Giardia* infections in reptiles are rarely pathogenic but may cause nephritis and intestinal lesions in chelonians (Ladds 2009).

Eimeria and *Isospora*

The coccidia (*Eimeria* spp.) of macropodids and wombats have been studied relatively intensely primarily because of their association with fatal, or at least debilitating, disease in their hosts (Barker *et al.* 1972, 1979, 1988a, 1988b, 1988c, 1989; O'Callaghan *et al.* 1998). However, the coccidians of few other groups of marsupials have been described even though they are known to be present (e.g. bandicoots). More recently, species of *Eimeria* have been described from the brushtail possum (*Trichosurus vulpecula*) (O'Callaghan and O'Donoghue 2001), the western barred bandicoot (*Perameles bougainville*) (Bennett *et al.* 2006), the boodie (*Bettongia lesueur*) (Hulst *et al.* 2016) and from the prostate of *Antechinus flavipes* at the time of male postmating immunosuppression and mortality (Amery-Gale *et al.* 2018). The latter novel coccidian develops extraintestinally rather than intestinally and sporulates endogenously rather than in the external environment. Further investigations of species of *Eimeria* from other than macropodid hosts may reveal additional novel life cycles.

Molecular analysis of the 18S SSU and COI genes of *E. macropodis* from the tammar wallaby (*Macropus eugenii*) combined with statistical analysis of oocyst traits confirmed it as

a single polymorphic species with heterozygous alleles (Hill *et al.* 2012). Analysis of 18S SSU indicated the presence of at least two alleles that may have been mistaken for distinct species of *Eimeria* without confirmation of heterozygosity by an alternative genetic marker. Analysis of gene sequences placed *E. macropodis* within the marsupial clade consisting of *E. trichosuri* from the mountain brushtail possum (*Trichosurus cunninghami*). Bayesian analysis confirmed that the marsupial species of *Eimeria* diverged before those from placental mammals, which is consistent with host evolution (Power *et al.* 2009). Subsequent studies (Ogedengbe *et al.* 2018) have confirmed these findings, placing the marsupial species basal to all remaining species of *Eimeria* in mammals and birds.

Although many eimeriids of endemic Australian birds, less so reptiles, have been described (O'Donoghue and Adlard 2000; Yang *et al.* 2012), life cycles and the diseases they may cause remain poorly known. Species of *Eimeria* primarily, but also *Isospora*, have been implicated in causing intestinal, hepatic and renal disease in birds (Harrigan 1981; Ladds 2009) but neither genus was associated with clinical disease in reptiles in the Northern Territory, Queensland or New South Wales (Cannon 1967).

Sarcocystis

The cysts or intermediate stages of *Sarcocystis* have been documented in a wide variety of marsupial and eutherian mammals, and birds in Australia (Munday *et al.* 1979; Harrigan 1981; O'Donoghue *et al.* 1987a; O'Donoghue and Adlard 2000) but few life cycles are known. Tiger snakes (*Notechis ater*) were identified as definitive hosts of *S. murinotechis* which occurs as cysts in several native and introduced rats (Munday and Mason 1980). The definitive hosts of the species of *Sarcocystis* occurring in the Macropodidae especially the larger members of the kangaroos and wallabies (*Macropus*, *Notamacropus* and *Osphranter*) remain speculative given the absence of large predators on the mainland, other than the dingo (*Canis familiaris*), and neither dingos nor other large predators occur in Tasmania. Microscopic and macroscopic cysts variously identified as belonging to the genera *Globidium*, *Ileocystis*, *Lymphocystis*, *Sarcocystis*, *Hammondia* or *Toxoplasma* have been described from the muscularis externa and the submucosa of the forestomach, intestinal mucosae and colon, muscularis externa of the oesophagus and caecum, and skeletal muscles of macropodid marsupials. The morphology of several of these originally thought to conform more to those of the genus *Globidium* are now thought to be megaloschizonts of *Eimeria* spp. (Pellérdy 1974; O'Donoghue *et al.* 1987a). Infection of the skeletal muscles of birds is relatively common (Harrigan 1981), indicating their potential role as intermediate hosts, but knowledge of the definitive hosts remains unknown. Acute disease in Australian native birds has been reported primarily from those in captivity overseas (Ladds 2009). Australian reptiles may be both intermediate and definitive hosts for species of *Sarcocystis*.

Toxoplasma

Toxoplasma gondii is a ubiquitous parasite of terrestrial and marine mammals and other vertebrates. The disease, toxoplasmosis, caused by this obligate intracellular coccidian

parasite is a significant cause of morbidity and mortality in captive marsupials although evidence for its impact on wild populations is equivocal (Canfield *et al.* 1990; Hartley *et al.* 1990; Obendorf and Munday 1990; Bettiol *et al.* 2000a; Donahoe *et al.* 2015a). *T. gondii* infection is non-pathogenic in wild eastern quolls (*Dasyurus viverrinus*), suggesting that this species may be considered a sentinel species for the threat of toxoplasmosis in susceptible endangered hosts in Tasmania (Fancourt *et al.* 2014). In a survey of the published literature, Hillman *et al.* (2016a) concluded that there was insufficient scientifically robust supporting evidence to indicate that *T. gondii* is a threat to the conservation of free-ranging marsupial populations in Australia. The geographical distribution of *T. gondii* may be Australia-wide, given the extensive range of feral cats, although dissemination by feral cats has been investigated only to a limited extent (Gregory and Munday 1976; Coman *et al.* 1981a; Fancourt and Jackson 2014). Mesopredator release of feral cats in Tasmania following the extensive decline of the apex predator, the Tasmanian devil, may be significant for endangered native species susceptible to *T. gondii* infection (Hollings *et al.* 2013).

Earthworms, a major component of the diet of eastern barred bandicoots (*Perameles gunnii*), are thought to act as paratenic hosts of *T. gondii*, passing oocyst-contaminated soil through their alimentary tracts (Bettiol *et al.* 2000b). Infection due to contaminated coastal freshwater runoff is considered an exposure source for marine mammals (Donahoe *et al.* 2014). Vertical transmission of *T. gondii* may occur in chronically infected marsupials (Parameswaran *et al.* 2009). Non-archetypal Type II *T. gondii* genotypes and atypical strains (Parameswaran *et al.* 2010; Donahoe *et al.* 2014, 2015a), and multiple infections in individuals (Pan *et al.* 2012) have been found in terrestrial and marine hosts with the suggestion that these forms may be more pathogenic.

Toxoplasmosis is much less common in birds than in mammals, O'Donoghue and Adlard (2000) listing infection in 11 species. Most cases come from companion, aviary or zoo birds, serology confirming that infections are often subclinical (Ladds 2009).

Atoxoplasmosis (= *Lankesterella* spp.) occurs in frogs, toads and birds and is a parasitic pathogen of passerine birds that is difficult to manage in captive birds (Ladds 2009). Although recorded in Australia, there is no report of clinically apparent atoxoplasmosis. Delvinquier (1989) reported *Lankesterella hylae* in the blood of the green tree frog, a protist reported to have many ultrastructural similarities to species of *Plasmodium*, *Toxoplasma*, *Sarcocystis* and *Lankesterella garnhami* (Stehbens 1966).

Besnotia, *Frenkelia* and *Hammondia*

O'Donoghue and Adlard (2000) listed *Besnotia wallacei* in cats, house mice and the two introduced species of rats, unidentified species of *Frenkelia* in the brown falcon (*Falco berigora*), southern boobook (*Ninox boobook*), Australian barn owl (*Tyto delicatula* (as *T. alba*)) and masked owl (*Tyto novaehollandiae*), and *Hammondia hammondi* in goats, cats, house mice, ship rats and the tammar wallaby (*Macropus eugenii*).

Haemosporida

Plasmodium, *Leucocytozoon*, *Haemoproteus* and *Polychromophilus*

The Haemosporida are an order of intraerythrocytic protozoan parasites that infect diverse vertebrate tissues and are vectored by diverse groups of biting Diptera. The major cladogenic events in this group seem to be associated with shifts between vector host families (Maia *et al.* 2016), although very little is known about the vectors of most members of the group in Australia. The dominant genera occurring in Australian wildlife are species of *Plasmodium* causing generally asymptomatic avian malaria in native and introduced birds, species of *Leucocytozoon* and *Haemoproteus* including frequent dual asymptomatic infections (Harrigan 1981; Hartley 1989; Ladds 2009) and *Polychromophilus melanipherus* in small bats, suspected of using nycterbiid flies as vectors (Mackerras 1959; Dew 1970). *Plasmodium mackerrasae* occurs in several species of skinks of the genus *Egernia* (Telford 1979).

Hepatocystis, *Johnspretia* and *Sprattiella*

This diverse group occurs in flying foxes (Megachiroptera: Pteropidae) in north Queensland. Two species of *Hepatocystis*, *H. levinei* and *H. pteropi*, occur in the three species of flying fox in Australia (Landau *et al.* 1985, 2012a, 2012b; Schaer *et al.* 2018). The life cycle of *H. levinei* has been completed in the biting midge, *Culicoides nubeculosus*, under laboratory conditions (Landau *et al.* 1985). The co-occurrence of *Johnspretia copmani*, *Sprattiella alecto* and a species of *Hepatocystis* have also been reported in the black flying fox (*Pteropus alecto*) (Landau *et al.* 2012a, 2012b). Species of *Hepatocystis* infect a range of primates and bats, and are close relatives of species of *Plasmodium* from mammals. Multilocus phylogenetic analysis of *Hepatocystis* spp. from species of *Pteropus* from Australia and Asia form a distinct clade that is sister to all other *Hepatocystis* spp. from primates and bats from Africa and Asia (Schaer *et al.* 2018).

Fallisia and *Bilbraya*

Fallisia copemani occurs in the skink *Carlia rhomboidalis* in the Daintree rainforest of north Queensland with up to 85% of lymphocytes estimated to be infected (Paperna and Landau 1990a). Double and even triple infection of cells with identical or different stages was common and macrogametocytes always outnumbered microgametocytes. Transmission in nature may be restricted to the acute and subacute periods of infection as it could not be maintained during the chronic phase due to the extreme disparity between male and female gametocytes.

Bilbraya australis was described from the gecko *Phyllodactylus marmoratus* in South Australia where parasitaemia was followed for six months (Paperna and Landau 1990b). Two stages featured in the blood, merogony lasting a month with massive infections of up to 12 parasites per erythrocyte in 95% of those circulating and resulting in severe anaemia. This was followed by massive gametogony lasting another month with gametocytes remaining in the blood for at least four months, reflecting a potentially long period of transmissibility.

The phylogeny of representative haemozoan species of the phylum Apicomplexa was reconstructed by cladistic analyses of ultrastructural and life-cycle characteristics of four apicomplexans (Jakes *et al.* 2003). There was no apparent correlation between parasite phylogeny and that of their vertebrate hosts, rather some relationship between parasites and their intermediate hosts. Evolutionary links appear more likely between the vectors of these parasites rather than between their very diverse range of vertebrate hosts.

There is a great deal more to be done in determining the genera of Haemosporida in Australian wildlife using a combination of ultrastructural, life-cycle and molecular analyses, their stages in both vertebrate and invertebrate vectors and their ecology and epidemiology in free-ranging populations before the systematics of the Apicomplexa can be satisfactorily resolved.

Myxozoa

Myxobolus

Myxozoans, found principally in the muscle, brain and gall bladder of their hosts, were originally classified as protozoans but are now recognised as metazoans and to have affinities with cnidarians (Nesnidal *et al.* 2013). They are known mostly for causing diseases in fish and the significant losses that may be incurred by commercial aquaculture (Lom and Dyková 2006). One of the best known of these is *Myxobolus cerebralis*, the causative agent of whirling disease in rainbow trout (Wolf and Markiw 1984; Lom and Dyková 2006).

Myxozoans are among the most common metazoan parasites found in fishes of the Great Barrier Reef, the fringing reefs of Western Australia and along the eastern coastline of New South Wales (e.g. Lom *et al.* 1992; Lom and Dyková 1994; Gunter *et al.* 2010; Heiniger *et al.* 2011). They also occur in reptiles, amphibians, waterfowl and small mammals in Australia. Two species of *Myxobolus* have been described affecting the liver, brain and urogenital system of Australian frogs (Johnston and Bancroft 1918; Browne *et al.* 2002). These species have now been reported in common (*Litoria caerulea*, *L. fallax*, *L. lesueuri*, *L. peronii*) and endangered (*L. aurea*, *L. raniformis*) frog species though only as incidental findings (Berger 2001; Mann *et al.* 2010). Given the distribution of these frog species it is likely that *Myxobolus* spp. will be found across all of the east coast of Australia.

Cystodiscus

Two species of *Cystodiscus* produce myxospores in the gallbladders of Australian frogs (Hartigan *et al.* 2012c). The potential impact of these parasites on the conservation of Australian frogs remains unknown but it has been suggested that myxosporean infections may represent a key threatening process contributing to amphibian decline (Sitjà-Bobadilla 2009; Hartigan *et al.* 2012c, 2013). These two species originally were thought to be a single species, *Cystodiscus immersus*, that was introduced to Australia with the exotic cane toad (*Rhinella marina*) (Hartigan *et al.* 2010, 2011, 2012b, 2012c). This hypothesis was put forward by Delvinquier (1986) after a survey of Australian frog gallbladders demonstrated similar myxospores to *C. immersus* in native Australian frogs and

R. marina. The hypothesis was not considered again until 2011 when genotyping of gallbladder myxospores and infected brain and liver tissue from several Australian frog species showed that the parasite thought to be *C. immersus* was in fact two novel parasites with similar spore morphology to each other and to *C. immersus* (Hartigan *et al.* 2011, 2012a, 2012c). Confirming the cryptic diversity of the two Australian endemic species required several descriptive tools including comparison of multiple rDNA regions, transmission and scanning electron microscopy as well as histopathology. *Cystodiscus australis* and *C. axonis* could be distinguished genetically and it was discovered that *C. axonis* had both liver and brain intra-axonal developmental stages (Hartigan *et al.* 2011, 2012a). Both species infect and cause disease in tadpoles although not all host species are affected in the same way (Hartigan *et al.* 2012c, 2013). The lesions caused by both species included inflammation and hyperplasia of the livers of frogs. Brain lesions attributed to *C. axonis* were more severe in some frog species (*Litoria booroolongensis*, *L. castanea* and *L. raniformis*) than others (Hartigan *et al.* 2012c). Frogs with severe disease exhibited neurological dysfunction, lost the ability to right themselves and in some cases lost hindlimb movement. It is speculated that the infection with *Cystodiscus* species may cause delayed metamorphosis leading to tadpole overwintering (Hartigan *et al.* 2012c) and the risk of predation or pond desiccation.

Helminths

Helminths (trematodes, cestodes, nematodes, acanthocephalans) represent an extraordinarily diverse array of internal parasites and, in contrast to some of the other taxonomically defined parasite groups, are better considered by host grouping rather than by host taxonomic affiliations as genera and families of helminths tend to be specific to a particular class of vertebrates.

Marsupials and monotremes

The marsupials and monotremes are the most obvious and most distinctive components of the Australian mammalian fauna and therefore it is of little surprise that they have been a significant focus of interest in the area of wildlife parasitology, abetted by the vast numbers of nematodes seen on opening many macropodid stomachs and the common occurrence of the large filarioid nematode *Pelecitus roemeri* in the intermuscular tissues of meat that might otherwise be destined for human or animal consumption.

The helminth fauna of marsupials and monotremes is exceptionally diverse (Beveridge and Spratt 1996). A recent review (Spratt and Beveridge 2016) listed over 600 species that had been described but also indicated many more awaiting description. The figure they provided (see fig. 1) suggested a small continuing increase in the number of marsupial species being described compared with a much greater increase in the number of parasite species being described.

In spite of this effort, no helminths have been reported from 26 species (10.2%) of marsupials and monotremes (Spratt and Beveridge 2016), suggesting that current estimates of species numbers are far from being comprehensive. Of those hosts from which parasites have been described, frequently only a small number of animals has been examined and limited opportunities

for sampling rare marsupial host species for parasites further limit the reliability of current estimates of biodiversity (Beveridge and Spratt 2015). An additional difficulty, identified by Beveridge and Gasser (2014), is the increasing recognition of the existence of cryptic species, identifiable by molecular technologies but not always by morphological methods. Examples of this phenomenon are the strongyloid nematode *Hypodontus macropi* found in the large intestine of kangaroos and wallabies which appears to be a complex of 10 species (Chilton *et al.* 2012), the common gastric nematode of macropodids, *Rugopharynx australis*, which was subdivided into 10 species based on morphological and genetic criteria (Beveridge and Chilton 1999) but within which additional cryptic species remain (Chilton *et al.* 2016), and the bile duct cestode *Progamotaenia festiva*, found in macropodids and wombats, within which seven species were described by Beveridge and Shamsi (2009), again based on morphological and molecular criteria but within which at least five cryptic species, identifiable genetically but not (currently) morphologically, remain unnamed (Beveridge *et al.* 2007). The presence of cryptic species within helminth groups is likely to be an ongoing issue in attempts to define the helminth fauna of monotremes and marsupials.

Apart from documenting the number of species present for analyses of biodiversity, an additional area of interest for the helminths of Australian mammals has been to try to determine their phylogenetic origins. Beveridge and Spratt (1996) suggested that in spite of the monophyly of the Australasian marsupials, the origins of their helminth parasites were probably highly diverse, some with potential connections to the parasites of South American marsupials, others with endemic vertebrates present on the continent when marsupials arrived and also more recent introductions with rodents and bats reaching Australia from Asia. Evidence for some connection between the South American and Australian marsupial fauna is provided by the cestode genus *Paralinstowia*, which occurs in didelphid marsupials in South America and peramelid marsupials in Australia (Beveridge and Spratt 1996). Both morphological and molecular evidence suggest that the endemic nematode family Mackerrastrongylidae may have its origins in echidnas, which presumably existed on the continent before the arrival of the marsupials, but subsequently invaded dasyurid and peramelid marsupials (Chilton *et al.* 2015). The original Australian marsupials were carnivores and therefore the presence of parasite groups primarily parasitic in herbivores can most readily be explained by the subsequent arrival of herbivores (rodents) from Asia. This seems to be the most likely source of both the anoplocephaline cestodes and the strongyloid nematodes of marsupials (Beveridge and Spratt 1996). In both instances, species have been identified in rodents (the cestode *Bertiella anapolytica* and the nematode *Cyclodontostomum purvisi*) which occur in Asia and in Australia (Beveridge and Spratt 1996). Additional examples of marsupial nematodes with an Asian distribution including parasites of bats are provided by Spratt (2007). For additional parasite groups, origins are either unknown or are contested, as is the case for the nematode subfamily Herpetostrongylinae with a South American origin proposed by Humphery-Smith (1983), an Asian origin suggested by Durette-Desset (1985) and the possibility of an origin in

monotremes (echidnas) indicated by molecular data (Chilton *et al.* 2015). Thus, the origins of the Australian marsupial helminth fauna are far from settled, but pose intriguing questions in the broader canvas of host–parasite evolution.

The evolution of helminth parasites has also been studied within the Australian context. Coevolutionary relationships between the herpetostrongyline nematodes and their marsupial hosts have been suggested based on morphological (summarised in Beveridge and Spratt 1996, fig. 8) and molecular (Chilton *et al.* 2015) data. Basal taxa occur in dasyurid marsupials, with subsequent diversification to the peramelids and then to the diprotodontids (possums, rat-kangaroos, wallabies and kangaroos). However, detailed studies remain to be undertaken. By contrast, studies of the anoplocephaline cestodes and cloacinid nematodes of macropodids using both morphological and molecular approaches currently suggest that host switching has been the major mechanism by which these large parasite radiations have evolved (Baverstock *et al.* 1985; Beveridge and Spratt 1996; Beveridge and Chilton 2001; Chilton *et al.* 2011, 2017).

The evolution of many groups of helminth parasites of marsupials remain unstudied, particularly using molecular methods, but provides considerable potential for additional basic studies of parasite evolution.

Two early reviews of disease in marsupials (Barker *et al.* 1963; Arundel *et al.* 1977) included diseases caused by helminths, with a more recent review by Ladds (2009) specifically documenting the helminths causing disease in these hosts. Spratt (2002) provided a review of the diverse parasites and pathology of the respiratory tracts of native and feral mammals in Australia. Most helminths present in marsupials and monotremes appear to be relatively non-pathogenic. However, Arundel *et al.* (1977, 1990) reported substantial mortalities in eastern grey kangaroos (*Macropus giganteus*) due to the nematode *Globocephaloides trifidospicularis*. Other nematodes in macropodids induce lesions in the gastro-intestinal tract, the lungs, the pericardium and the intermuscular connective tissues, but their pathological significance is not well understood (Ladds 2009). The increase in the number of helminths in male *Antechinus agilis* associated with their mortality was investigated by Barker *et al.* (1978), but it was concluded that helminths played a limited role in the deaths of their immuno-suppressed hosts.

The two introduced parasites, *E. granulosus* and *F. hepatica*, also cause significant disease, including death, in some species of marsupials in endemic areas (Spratt and Presidente 1981; Johnson *et al.* 1998; Presidente (pers. comm.) in Obendorf and Black 1983). However, elucidating the role of helminths inducing disease in marsupials remains a significant area for further investigations.

Rodents

The helminth parasites of rodents in Australia were reviewed by Smales (1997) although substantial advances have been made since then both in documenting the fauna in Australasia and in examining the structure of the helminth communities present (see references in Smales and Spratt 2008). Studies of the rodent fauna have been relatively neglected in favour of those of the more visible marsupials (Warner 1998), but provide particular

insights into the evolution of the helminth fauna of Australian mammals. Rodents reached Australia from New Guinea in multiple invasions, possibly up to 5 million years ago (Rowe *et al.* 2008), bringing many helminths with them. Some of these helminth groups apparently switched to marsupials (Beveridge and Spratt 1996; Warner 1998). A fuller understanding of the evolution and dispersal of the parasites of Australian rodents requires a more detailed knowledge of those parasitic in rodents in New Guinea and extensive studies of this topic are summarised by Smales (2012).

From a human health perspective, one important parasite of introduced rodents is the nematode *Angiostrongylus cantonensis*, which causes eosinophilic meningitis in humans (Spratt 2005). The parasite uses gastropods as intermediate hosts and is exceptionally catholic in its definitive hosts, occurring in domestic animals, marsupial and eutherian wildlife as well as birds, aberrant hosts that often exhibit clinical signs of paralysis and paresis (see Spratt 2015, table 2). It occurs in metropolitan areas of Brisbane and Sydney, where it has been suggested that tawny frogmouths and brushtail possums may serve as biosentinels (Ma *et al.* 2013). *A. cantonensis* plays a potentially devastating role in and around zoos and fauna parks where captive rearing of endangered species programs may exist and where control of *Rattus* spp. is invariably difficult (Spratt 2015).

The nematode *Calodium hepaticum* (as *Capillaria hepatica*) was employed as a potential agent in the biological control of mouse plagues caused by *Mus domesticus* in the wheat-growing regions of southern and eastern Australia (Singleton *et al.* 1995; Singleton and Chambers 1996). Manipulative field experiments were conducted on the Darling Downs, Queensland, and in the central Mallee wheatlands of Victoria. Although there was effective transmission of the parasite, in one instance for 4.5 months, it was associated with a significant reduction in prevalence of infection in the populations with time. The conclusions from the studies indicated that *C. hepaticum* will not limit mouse populations if released into a low-density population during a long dry period and that greater knowledge of the factors influencing survival and transmission of the parasite under field conditions was essential.

Bats

The helminths of Australian bats have been very poorly studied in spite of the fact that overseas work indicates that microbats generally harbour quite an extensive helminth fauna. A major study of the nematode *Nycteridostrongylus unicollis* is contained within the Ph.D. thesis of I. Humphery-Smith (1982), but the work has not been published. The large bats, the flying foxes, harbour relatively few parasitic helminths but the life cycle of the ascaridoid nematode *Toxocara pteropodis* has been studied by Prociv (1989), who showed that transmission was primarily transmammary.

Marine mammals

Studies of the helminth fauna of Australian marine mammals are relatively limited and the species present were reviewed by Arundel (1978). Since then, the parasites of phocids (seals and sea-lions) have been further investigated, primarily due to pup mortality caused by the hookworm *Uncinaria stenocephala*

(see Marcus *et al.* 2014), while the potential pathological impact of the lungworms *Parafilaroides normani* and the gastric ascaridoid *Contracaecum ogmorhini* remain to be determined (Arundel 1978; Nicholson and Fanning 1981; Ladds 2009). There has been little published on the parasites of cetaceans apart from a study of the lungworms of dolphins and their pathological significance (Tomo *et al.* 2010). A review of the helminth parasites causing disease in cetaceans, pinnipeds and the dugong has been published by Ladds (2009). Otherwise, the helminth parasites of Australasian pinnipeds and cetaceans remain relatively poorly studied.

Native eutherian carnivores – the dingo

The parasites of the dingo have been particularly well studied because of its role as the definitive host in a sylvatic cycle of the hydatid tapeworm *Echinococcus granulosus* involving dingoes and macropodids. The distribution and prevalence of *E. granulosus* was reviewed by Schantz *et al.* (1995). The parasite is prevalent in dingoes in the high-rainfall forested areas of eastern Australia (Queensland: Durie and Riek 1952; Baldock *et al.* 1985; New South Wales: Gemmell 1959; Jenkins and Morris 1991; Victoria: Coman 1972b), while in northern Queensland, the incursion of dingoes infected with *E. granulosus* into regional towns represents an additional public health risk (Brown and Copeman 2003). *Echinococcus* infection was successfully eradicated in Tasmania (Beard *et al.* 2009) due to the lack of a significant sylvatic cycle. It is currently not possible on the mainland due primarily to the persistent sylvatic cycle between dingoes and macropodids (Schantz *et al.* 1995).

The remaining parasites found in dingoes are those commonly found in domestic dogs (Coman 1972b). However, the tracheal nodule worm *Oslerus osleri* and the nasal-cavity-inhabiting pentastome *Linguatula serrata* are both found at a very high prevalence in dingoes, while they are uncommon in domestic dogs (Dunsmore and Spratt 1979; Shamsi *et al.* 2017).

Feral carnivores – foxes and cats

Possibly because of their potential role as reservoirs of parasites of domestic animals, the helminth fauna of both foxes and feral cats has been relatively well studied (e.g. cats: Coman 1972a; Coman *et al.* 1981b; Gregory and Munday 1976; Ryan 1976a; O'Callaghan and Beveridge 1996; Milstein and Goldsmit 1997; foxes: Coman 1972b; Ryan 1976b). Both host species are infected with the common helminths of domesticated dogs and cats respectively, such as the cestodes *Taenia pisiformis*, *T. serialis*, *Hydatigera taeniaeformis*, *Spirometra erinaceieuropaei* and *Dipylidium caninum* and the nematodes *Toxocara canis*, *T. cati*, *Toxascaris leonina* and *Aelurostrongylus abstrusus*, as might be expected. In addition, *Echinococcus granulosus* has been found in a relatively small number of foxes (see summary in Schantz *et al.* 1995), presenting a public health risk in certain areas.

However, the spirurid nematode *Cylicospirura felineus*, while common in feral cats, is rare in domestic cats and *Cyathospirura seurati* (formerly *C. dasyuridis*) (see Hasegawa *et al.* 1993) infects both foxes and cats as well as dasyurid marsupials (Mawson 1968). The former is a cosmopolitan species of cats while the latter has a widespread distribution in Asia (Hasegawa *et al.* 1993). By contrast, the acanthocephalan

Oncicola pomatostomi, while prevalent in both foxes and feral cats and having birds as secondary intermediate hosts (Mawson *et al.* 1986), appears to be endemic. The phylogenetic origins of this parasite remains to be determined.

Lagomorphs

The helminth parasites of introduced lagomorphs have been extensively studied, in part due to the possibility of using helminths as a means of controlling lagomorph populations. All helminths were introduced with their hosts and, perhaps not surprisingly, their parasite fauna is less diverse in Australia, in particular, the absence of helminths with indirect life-cycles, metastrongyloid nematodes and anoplocephalid cestodes. Initial surveys of both rabbits and hares (Mykutowycz 1956; Hesterman and Kogon 1963) were followed by detailed studies of the ecology of individual nematode species (see summary in Dunsmore and Dudzinski 1968). The decline in research generally on rabbits in Australia has been accompanied by a decline in interest in their parasites and, apart from reports of sheep nematodes infecting rabbits (Tai *et al.* 2013), little work has been undertaken in this field recently.

Feral ungulates: goats, camels and pigs

Studies on the parasites of feral goats are quite limited (McKenzie *et al.* 1979; Beveridge *et al.* 1987). The helminths encountered in these surveys were essentially parasites shared with sheep, apart from two species, *Camelostrongylus mentulatus* and *Nematodirella dromedarii*, which are primarily parasites of camelids. There are even fewer records of parasites of wild camels, with Barton (2008) reporting the occurrence of *N. dromedarii* and the ruminant nematode *Cooperia pectinata* from camels in central Australia.

Surveys of the parasites of feral pigs are likewise limited, with available records of parasites being similar to those found in domestic pigs (Pavlov 1988; Heise-Pavlov and Heise-Pavlov 2004). The most important helminth issue pertains to the occurrence of larval stages (spargana) of the cestode *Spirometra erinaceieuropaei*, which may result in zoonotic infection in humans who ingest improperly cooked feral pig.

Birds

The known helminth fauna of Australian birds was summarised in the checklist of Mawson *et al.* (1986), in which they recognised 142 fully identified species of trematodes, 93 cestodes, 220 nematodes and 14 acanthocephalans, indicating the presence of an extremely diverse fauna. As important are the numerous records of incompletely identified species, suggesting that the helminth fauna of birds is far from being fully determined. Due to the personal interest of these authors, the nematodes, trematodes and acanthocephalans were treated in greater detail. There have been additional studies of bird helminths since the publication of the checklist, but documenting the helminth fauna of Australian birds remains a substantial task and Australian avian cestodes were recently identified as an extremely poorly known component of the global cestode fauna (Mariaux *et al.* 2017; Mariaux and Georgiev 2018).

Given recent studies on the phylogeny of birds and the significance of the Australasian region in their evolution

(Barker *et al.* 2004), phylogenetic studies of the helminth parasites of Australasian birds are almost entirely lacking and would appear to be a potentially highly rewarding area for future parasitological investigations. The role of helminths in diseases of native birds is poorly understood and warrants significant attention (Harrigan 1978, 1981; Ladds 2009).

Reptiles

The current status of knowledge of the helminth parasites of Australian reptiles has been summarised in a checklist by Pichelin *et al.* (1999). Much of the information available has been assembled through incidental collections, although the extensive ecological and taxonomic studies of Jones (2014), particularly on the parasites of varanids, those on gekkonids (Goldberg and Bursey (2001) and the experimental studies of Sprent (e.g. Sprent and McKeown 1979) on the ascaridoid nematodes of pythons stand out as landmarks in the field. Similarly, the detailed life-cycle studies of reptilian cestodes by Hickman (1963) stand out as an additional landmark but in a somewhat different field. More recent ecological studies on the ways in which the social behaviours of reptiles affect parasite transmission have opened new windows into the ecology of reptile helminths (Fenner *et al.* 2011) and provide a pathway to further such investigations. Not only is the extent of the helminth fauna of Australian reptiles yet to be determined, phylogenetic studies of their origins as well as studies of associated disease are extremely limited (Ladds 2009).

Amphibians

The checklist of helminth parasites of amphibians by Barton (1994) indicates clearly the deficiencies in knowledge of parasites of this group of animals. Extensive collections of unidentified trematodes, cestodes and nematodes are held in the Australian Helminthological Collection of the South Australian Museum awaiting study. Inglis (1968) published an intriguing study on the biogeographical relationships of nematode parasites of frog species on either side of the Nullarbor Plain, but his interesting observations have not been pursued. Recent studies on the lung-inhabiting nematode *Rhabdias pseudosphaerocephalus* have shown that it is more pathogenic in the introduced cane toad than in several native species of frogs and its potential as an agent to control cane toads has been suggested (Pizzatto *et al.* 2010).

Arthropods

This area of wildlife parasitology includes ticks, mites, fleas and lice, and, to a lesser extent, flies. Each of these taxonomic groups is considered in turn.

Ticks

Undoubtedly, the most significant studies of the ticks of Australian vertebrates were those of F. H. S. Roberts, culminating in his monograph 'Ticks of Australia' (Roberts 1970). Since then, activity in this field has been sporadic and overshadowed by research on ticks of veterinary importance such as the cattle tick, *Rhipicephalus (Boophilus) australis* (formerly *Boophilus microplus*).

A small number of additional tick species has been added to the Australian fauna since the publication of Roberts' monograph (e.g. *Amblyomma vikirri*: Keirans *et al.* 1996; *Amblyomma cyprium*: Kemp and Wilson 1979; *Argas* spp.: Hoogstraal and

Kaiser 1973; Kaiser and Hoogstraal 1974; *Ixodes woyliae*: Ash *et al.* 2017), indicating that the documentation of the Australian tick fauna is far from complete.

Significant ecological and genetic work has continued if on a somewhat sporadic basis. Substantial long-term ecological studies have been published on the lizard ticks (*Bothriocroton* (formerly *Aponomma*) *hydrosauri*, *Amblyomma limbatum* and *A. albolimbatum*) by Michael Bull and his colleagues (summarised in Godfrey and Gardner 2017). Their establishment of an extremely well defined parapatric boundary between these tick species across South Australia has been the source of numerous studies to determine how such a parapatric boundary might be maintained and which has provided numerous insights into the ecology of the tick species involved, although the precise mechanisms involved in the maintenance of the parapatric boundary remain to be elucidated (Godfrey and Gardner 2017).

Additional ecological studies have been published on individual species such as the kangaroo ticks *Ornithodoros gurneyi* (see Doube 1975) and *Amblyomma triguttatum* (see Guglielmone 1990) as well as *Ixodes tasmani* (see Murdoch and Spratt 2005), *I. hirsti* (see Oorebeek *et al.* 2009; Laan *et al.* 2011) and *I. holocyclus* (see Doube 1979). Distributional studies have examined the paralysis ticks *I. holocyclus* and *I. cornuatus* (Jackson *et al.* 2007).

Genetic studies have established the validity of the paralysis tick *I. cornuatus*, once thought to be a subspecies of *I. holocyclus* (see Jackson *et al.* 2000; Song *et al.* 2011) and *Aponomma tachyglossi* (now *Bothriocroton tachyglossi*) from echidnas in Queensland (Andrews *et al.* 2006). In addition, studies have been undertaken on the adverse effects of ticks on marsupials (Gemmell *et al.* 1991; Vilcins *et al.* 2005). Barker and Walker (2014) have recently reviewed in detail the ticks affecting humans and domestic animals in Australia.

However, this important field is in need of more sustained taxonomic and ecological interest. The recent erection of the genus *Bothriocroton* for several species of endemic Australian ticks parasitic on mammals, now thought to be extremely primitive in an evolutionary sense (Barker and Murrell 2002), suggests that studies of their biology could be extremely fruitful.

Mites

The seminal work on the parasitic mite fauna of Australia has been that of R. (Bob) Domrow, working at the Queensland Institute of Medical Research, and elegantly summarised in a series of reviews published before his retirement (Domrow 1987, 1991, 1992; Domrow and Lester 1985). In spite of occasional publications investigating the role of mites in disease (*Thaddeua* in wallabies and bettongs: Skerratt *et al.* 2007; Portas *et al.* 2015; *Eutrombicula* in wallabies: Old *et al.* 2009; sarcoptiform mites in *Dasyurus maculatus*: Vilcins *et al.* 2008; *Macropododicoptes* in *Wallabia bicolor*: Bochkov 2012), there has been limited sustained interest in these parasites until recently when sarcoptic mange caused by the introduced mite *Sarcoptes scabiei* in wombats has been recognised as a potentially threatening disease to small, isolated populations of both common and hairy-nosed wombats (Skerratt 2005; Simpson *et al.* 2016) as well as a potentially significant disease in koalas (Fraser *et al.* 2017; Speight *et al.* 2017).

In spite of the significant achievements of Domrow, new species of parasitic mites are being encountered (e.g. Lorch *et al.* 2007), but there is now limited taxonomic capacity in Australia for the description of such new species.

Fleas

The monograph of Dunnett and Mardon (1974) marked a significant point in the study of Australian fleas, but this area of research has subsequently received little attention. Some members of the endemic fauna, such as *Uropsylla tasmanica*, a parasite of the quolls *Dasyurus viverrinus* and *D. maculatus*, exhibit a remarkable life-cycle with the larval stages subcutaneous parasites of their hosts (Pearse 1981; Vilcins *et al.* 2008). It is likely that more unique biological phenomena will be discovered when the biology of more species is investigated.

Lice

Over the decades there has been relatively little activity in the taxonomy of parasitic lice by Australian workers. The bulk of the highly diverse avian louse fauna has been described by overseas workers, as has much of the fauna on marsupials. The louse fauna of Australia has been summarised by Palma and Barker (1996). The monograph on the lice of marsupials by von K  ler (1971) represented a significant advance and has been followed by revisions of the lice of rock-wallabies by Clay (1981) and Barker (1991a). Barker (1991b) utilised these studies to examine the evolution of lice on rock wallabies and to conclude, contrary to a widely held view at the time, that coevolution was not the primary mechanism of parasite evolution.

More recently, the lice of rodents have been reinvestigated by Weaver and Barton (2008) and Weaver (2017) with the descriptions of new species of *Hoplopleura*.

There have been no detailed studies of the ecology of lice of native animals apart from the exceptional work of Murray and his colleagues (Murray and Nicholls 1965; Murray *et al.* 1965) on the ecology of the lice *Antarctophthirus* and *Lepidophthirus* of Antarctic seals.

Clearly, the lice of Australian vertebrates present obvious opportunities for additional fruitful studies.

Flies

Parasitic flies are relatively few in number and this is to some extent also reflected in the lack of research interest in them. The botflies, Oestridae, while common in sheep and horses are represented by only a single species in native animals, *Tracheomyia macropi*, a parasite of the trachea and bronchi of kangaroos, which has been studied by Mykytowycz (1963). In addition, the introduced *Cephalopina titillator* is a common nasal bot in camels (Spratt 1984). Numerous species of mosquitoes, simuliids and ceratopogonids feed on native vertebrates and these have been studied relatively intensely because many of them also feed on humans and domestic animals, and are involved in disease transmission.

Hippoboscids are common parasites of birds in Australia with a few species occurring on macropodids. The most recent review of this group by Maa (1963) is now dated, but there has been no significant additions to his work since then.

Pentastomida

Adult pentastomids, commonly called tongue worms on account of their shape, are obligatory parasites of amphibians, various reptiles, birds, and marsupial and eutherian mammals including humans. Adults inhabit the respiratory tracts (lungs, nasal passages and tracheae) of their hosts. The above-mentioned host groups, some fish and at least one insect species may serve as intermediate hosts. The Pentastomida are now recognised as being related to the branchiuran crustaceans, as originally proposed by Van Beneden (1848) (Riley *et al.* 1978) or are a transitional group between the Arthropoda and Nematoda/Nematomorpha (de Oliveira Almeida and Christoffersen 1999).

Riley *et al.* (1985) provided an historical review of the records of pentastomids occurring in Australian reptiles and mammals. Poore and Spratt (2012) provided a detailed exposition of the known genera and species of Pentastomida occurring in Australian hosts as well as known intermediate hosts, including unpublished records. Two orders are recognised, the Cephalobaenida and the Porocephalida. The former is represented in Australia by the multispecies genus *Raillettiella*, occurring in agamid and scincid lizards, amphibians and elapid snakes, and the monotypic *Yelirella* from the lungs and nasal sinus of the marsupial sugar glider (*Petaurus australis*). The Porocephalida is represented by the genera *Sebekia*, *Alofia*, *Selfia* and *Leiperia* in crocodiles, *Parasambonia* in elapid snakes, *Elenia* in varanid lizards, *Waddycephalus* in elapid, colubrid and boid snakes, *Armillifer* in boid and colubrid snakes and *Linguatula* in the frontal sinuses of dogs, dingoes, foxes and the marsupial spotted tailed quoll (*Dasyurus maculatus*) in Victoria.

Three recent publications are noteworthy. Using combined morphological, allometric and molecular approaches Kelehear *et al.* (2011) demonstrated that *Raillettiella frenatus* is capable of maturing in both lizards and anurans. More importantly, they demonstrated that morphological features used in pentastomid taxonomy change as the parasite transitions through developmental stages in the definitive host, rendering as dubious previous descriptions of species based exclusively on morphology. Barton and Morgan (2016) provided the first records and descriptions of the infective nymphs of the pentastomes of crocodiles, *Alofia merki* and *Sebekia purdieae*, as well as other nymphs belonging to the family Sebekidae from four fish species from Western Australia, Northern Territory and north Queensland. Shamsi *et al.* (2017) reported prevalences of *Linguatula* cf. *serrata* in wild dogs (67.6%), red foxes (14.5%) and cattle (4.3%) in south-eastern New South Wales, the Australian Capital Territory and Victoria but nymphs were not found in a small number of feral pigs, rabbits, goats and a hare examined. Given these prevalence figures, they suggested that the search for the main intermediate host in the region should continue. Nymphs of *L. serrata* have been found in rabbits in south-eastern New South Wales and the endangered nail-tail wallaby (*Onychogalea fraenata*) in central Queensland (authors' pers. obs.).

Discussion

Wildlife parasitology is a highly diverse area of research and encompasses many fields including taxonomy, ecology, pathology and epidemiology. In addition, the organisms studied

are highly dissimilar in themselves, ranging from platyhelminths, nematodes and acanthocephalans to insects, arachnids, crustaceans and protists. As a consequence, researchers in this general field come from extremely disparate disciplines.

The overview presented above illustrates some of the diversity of themes within this very broad discipline area. First, the diversity of parasites of wildlife is far from being fully documented. This is not unexpected as Australia is recognised as a region of high biodiversity (CSIRO 2014), but such recognition does not always extend to parasites. The challenge to document the diversity of parasites in Australia continues at a traditional level, particularly with the problem of diminishing taxonomic expertise (Beveridge and Gasser 2014), but the advent of molecular methods has heightened the significance of this issue, with modern methods providing an avenue for major advances in documenting and restructuring the phylogeny of protistan parasites. At the same time they both complicate and facilitate the recognition of helminth parasites, which have traditionally been based on morphological methods, but within which species complexes are more readily identifiable using molecular methods. The current review identifies broad parasite taxa in which substantial advances are being made while at the same time identifying parasitic groups in which there is currently no such sustained activity.

Reliable identification of parasites is simply the first stepping stone to ecological and other studies. With a small number of notable exceptions, the biology of lizard ticks being one obvious example, knowledge of the life cycles, ecology and general biology of most parasites of wildlife are extremely poorly understood. Similarly, while the phylogenetic origins of the Australian vertebrate fauna are complex, so too are the likely origins of their parasites, which do not necessarily mirror that of their hosts. This fascinating aspect of parasite evolution has been addressed as a continuing area for research in the case of helminths (Beveridge and Spratt 1996), but remains to be addressed for most of the other parasitic groups.

The role of parasites as agents of disease has received relatively limited attention and in the past has been directed primarily to introduced parasites potentially transmissible to livestock (*E. granulosus*, *F. hepatica*). The recognition of significant diseases in wildlife due to endemic parasites such as species of *Trypanosoma* and *Globocephaloides* in macropodoids and introduced species such as *Sarcoptes scabiei* in wombats and koalas should lead to further investigations of parasites as agents of disease in wildlife.

The study of parasites of wildlife is not generally perceived as being of great social benefit and as a consequence funding opportunities for research in this area are limited. Not surprisingly, much of the research reported here has been opportunistic rather than being carefully designed. Two obvious exceptions are the long-term studies of the distribution of lizard ticks for which Michael Bull managed to attract funding from the Australian Research Council (see Godfrey and Gardner 2017), and a long-term study of the helminth communities of small marsupials by Spratt (1987), funded then by CSIRO but which would be unlikely to be considered for funding by that organisation in the current scientific climate. This area of research will probably remain, as it has been in the past, largely opportunistic, with individuals driven primarily by intellectual

curiosity, but without reliable sources of funding, conducting research as best they are able to with limited resources. The positive aspect of this review is to reveal just how much there is still to learn about the parasites of Australian wildlife, including parasites of major animal welfare significance, and how much has been and can be accomplished by interested individual scientists without significant long-standing financial support.

Conflicts of interest

The authors declare no conflicts of interest.

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