



Parasites of wombats (family Vombatidae), with a focus on ticks and tick-borne pathogens

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Abstract

Ticks (Arachnida: Acari) are vectors for pathogens and the biggest threat to animal health. Many Australian ticks are associated with pathogens that impact humans, domestic animals and livestock. However, little is known about the presence or impact of tick-borne pathogens in native Australian wildlife. Wombats are particularly susceptible to the effects of the ectoparasite *Sarcoptes scabiei* which causes sarcoptic mange, the reason for which is unknown. Factors such as other ectoparasites and their associated pathogens may play a role. A critical understanding of the species of ectoparasites that parasitise wombats and their pathogens, and particularly ticks, is therefore warranted. This review describes the ectoparasites of wombats, pathogens known to be associated with those ectoparasites, and related literature gaps. Pathogens have been isolated in most tick species that typically feed on wombats; however, there are minimal molecular studies to determine the presence of pathogens in any other wombat ectoparasites. The development of next-generation sequencing (NGS) technologies allows us to explore entire microbial communities in ectoparasite samples, allowing fast and accurate identification of potential pathogens in many samples at once. These new techniques have highlighted the diversity and uniqueness of native ticks and their microbiomes, including pathogens of potential medical and veterinary importance. An increased understanding of all ectoparasites that parasitise wombats, and their associated pathogens, requires further investigation.

Keywords Tick · Ectoparasite · Australia · *Acari* · Tick-borne · Pathogen · Wombat

Introduction

Collectively, ticks are major vectors of blood-borne pathogens for their vertebrate hosts. As a group, ticks transmit the greatest diversity of animal and human pathogens of any arthropod vector (de la Fuente et al. 2008). They pose the biggest arthropod threat of all vectors to pets and livestock, and pose the second biggest threat to humans, following mosquitoes (Pfäffle et al. 2013). Ticks have the ability to cause disease in their host either by direct means (e.g. tick paralysis, mammalian meat allergy), or more significantly by serving as a vector for pathogenic microorganisms such as bacteria,

viruses, protozoa and helminths to their vertebrate hosts (Estrada-Peña 2015). In addition, ingestion of ticks during grooming is a viable mode of transmission for some viruses in the Northern Hemisphere (Gilbert et al. 2004). While ticks are typically regarded only as vectors of pathogens, they can also act as reservoirs if the pathogenic organisms can be transmitted both transovarially (from adult to egg) and transstadially (survives moulting) (Raoult and Roux 1997). Furthermore, the typical multiple-host life cycle of most ticks combined with extensive feeding periods of 2–15 days means that many ticks and their pathogens can be distributed widely by their hosts' movements (Halsey and Miller 2018). Despite these factors, a comprehensive examination of the role these organisms may play in disease transmission and their impact upon native Australian fauna has not been undertaken (Vilcins et al. 2005).

Pathogenic microorganisms have co-evolved with both invertebrate vectors and vertebrate hosts over a long time period and have consequently developed various strategies to exploit their hosts' biology to succeed. One example is the relationship between tick salivary glands and pathogen transmission

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(Bowman and Sauer 2004). While feeding, ticks will alternate between injecting a solution of anticoagulant, immunosuppressive compounds and consecutively ingesting their blood meal. Pathogen transmission occurs between parasite and host when microorganisms invade the ticks' salivary glands and are injected into the vertebrate host throughout feeding (Šimo et al. 2017). Uninfected ticks likewise acquire pathogens in the same manner and this innovation is so effective that horizontal pathogen transfer often occurs when multiple ticks will simultaneously cofeed on a vertebrate host (Jones et al. 1989).

The ticks and associated pathogens of native Australian fauna have received little attention in comparison to those of humans and domestic animals. Native ticks and their vertebrate hosts have a unique evolutionary history, resulting in fauna and pathogens that are phylogenetically distinct in different geographical locations. Native fauna and ticks are also considered reservoirs for pathogens of medical and veterinary importance. Other ectoparasites such as lice, fleas and mites have received even less attention regarding their pathogenic potential. With most vector-borne diseases originating or being maintained in wildlife populations, it is of public health importance that the ectoparasites and their associated pathogens of native Australian fauna receive further attention.

The bare-nosed wombat (*Vombatus ursinus*) is distributed across the coastal regions of south-eastern Australia and into Tasmania (Fig. 1) (McIlroy 2008). One of the greatest parasitic threats to bare-nosed wombats is sarcoptic mange

(Skerratt et al. 1998), a disease spread by the burrowing mite *Sarcoptes scabiei*, which occurs throughout their entire range (Old et al. 2018), and has led to significant declines in some populations in New South Wales (NSW) and Tasmania (Martin et al. 1998). Given the threat posed by sarcoptic mange for wombats at both individual and population levels, there is a need to understand the relationship between wombats, their ectoparasites and their pathogens. The main objective of this review is to provide a reference tool for researchers and wildlife carers, update our understanding of wombat disease and wombat-ectoparasite relationships and highlight the gaps in knowledge relative to tick-borne disease in wombats. Hence, this review aims to highlight all known ectoparasites of Australian wombats, the pathogens known to be associated with these ectoparasites, and the impact that these pathogens may have on wombats is discussed. Particular emphasis is placed on wombat ticks due to their significance as a vector and their similarity to *Sarcoptes* mites.

Methods of review

Literature applicable to this study was located using formal search methods including textbooks, electronic databases and personal contacts. A systematic database review of published and publicly available literature was performed, complying with Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al. 2009). A

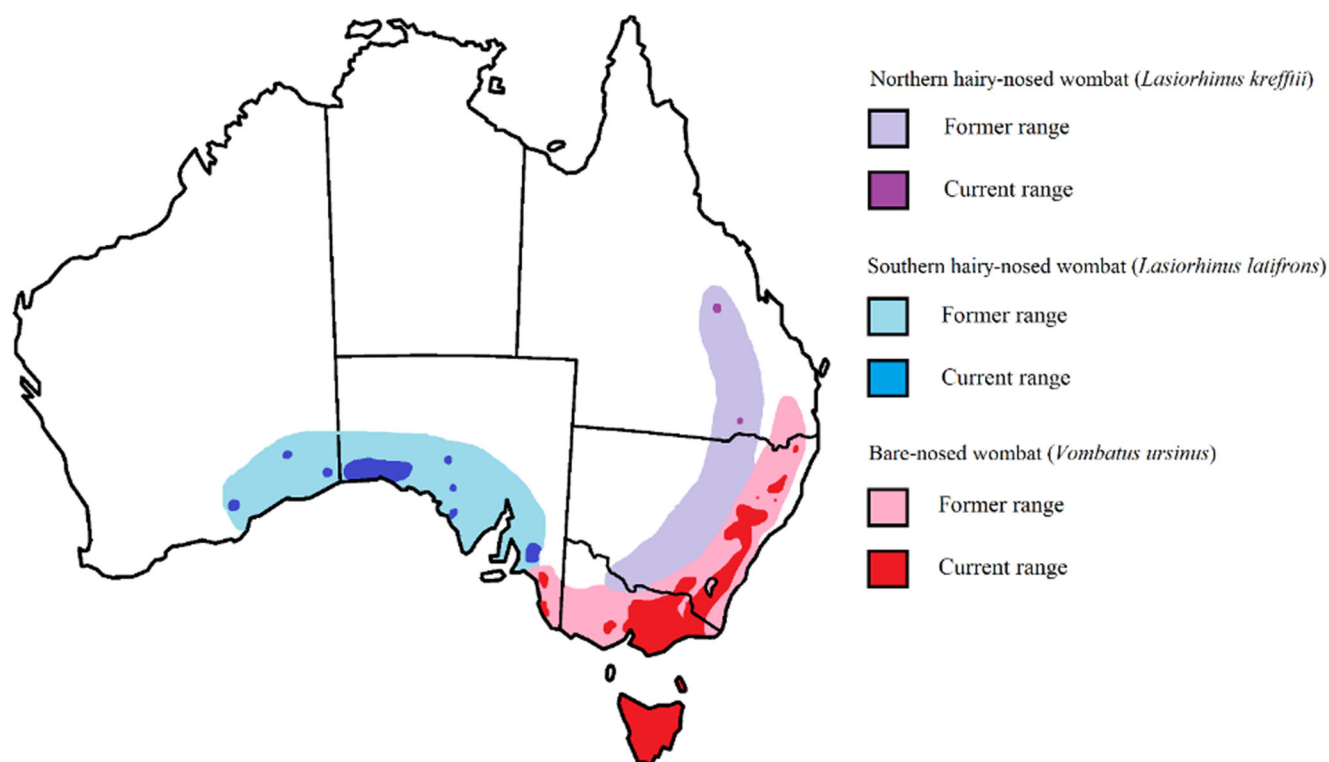


Fig. 1 Current and former distribution of the three extant species of Australian wombats

variety of electronic online databases were utilised including Science Direct and PubMed/Medline using primary keywords “Australia”, “tick”, “wombat”, “pathogen” and “microbiome”. No date or language restrictions were placed on search results.

Australian ticks

Australia has a unique evolutionary history with ticks, in addition to distinct climatic and environmental conditions favourable for six of the eight subfamilies of ticks. Of the almost 900 recognised tick species worldwide, 79 species are recognised in Australia (Ash et al. 2017; Barker 2019; Barker and Walker 2014; Kwak et al. 2018). Seventy-three tick species occur only on the Australian continent and its islands, and the remaining six species (*Rhipicephalus microplus*, *Otobius megnini*, *Argas persicus*, *Amblyomma breviscutatum*, *Rhipicephalus sanguineus* and *Haemaphysalis longicornis*) were introduced to Australia with humans and domestic animals during the past 230 years. At least 17 Australian tick species have been associated with humans (Graves and Stenos 2017). However, there is a lack of detailed information regarding Australian tick life cycles (Barker and Walker 2014) and it is assumed that like most Northern Hemisphere species, Australian ticks also feed mainly from three hosts. New hosts are regularly being recorded for Australian tick species (Barker 2019; Krige et al. 2018; Kwak et al. 2017) and the only ticks to have their genome and microbiome thoroughly investigated are those which parasitise humans, pets and livestock (Burnard and Shao 2019; Greay et al. 2018a).

Australian tick-borne pathogens

A majority of important human tick-borne illnesses, including Lyme disease and tick-borne encephalitis, occur only in the Northern Hemisphere. The *Ixodes ricinus* species complex is the most significant vector of pathogens in the USA (Oliver 1996), and the blacklegged tick (*I. scapularis*) is the most significant tick vector in Europe (Eisen and Eisen 2018), both of which have yet to be recorded in Australia (Barker and Walker 2014). Despite extensive studies into arthropod vectors worldwide, little is known about the impact of ectoparasites as vectors of disease on wombats and most other native Australian mammals (Vilcins et al. 2005). Being an isolated continent, Australia is relatively free of infectious bacterial tick-borne pathogens (TBPs) known to infect people, with only four TBPs causing human disease (Dehghani et al. 2019), and multiple non-infectious illnesses caused by tick bites (Beaman 2018). The Australian invertebrate and vertebrate fauna have co-evolved (Nava et al. 2009), and each

species has also evolved their own unique microbiomes. The six species of ticks which have been introduced into Australia have brought with them pathogens from other countries which cause disease in humans and both domestic and livestock species. These introduced tick species have been extensively studied due to their impact on health and the economy worldwide; however, little is known about the consequences that these introduced species have on native fauna, which have had little exposure to exotic ticks and their pathogens. Even less is known about the native species of ticks which are solely associated with native fauna.

Bacteria

Bacteria are the most studied TBPs worldwide and the only tick-associated pathogens to have been detected in ticks from wombats (Vilcins et al. 2009c). Bacterial pathogens are responsible for the vast majority of tick-borne infections, with a large proportion of these caused by tick-borne Rickettsiales (class Alphaproteobacteria), such as *Anaplasma*, *Ehrlichia*, *Borrelia* and *Rickettsia*. Currently in Australia, there are four human diseases caused by bacterial TBPs recognised: Queensland tick typhus, Flinders Island spotted fever, Australian spotted fever and Q-fever. Species of *Ehrlichia* and *Anaplasma* have been suggested as the cause of haematological disease in many species of mammal, particularly wild and domestic canines (Shaw et al. 2001). Until recently however, the only species of *Ehrlichia* and *Anaplasma* reported in Australia were introduced to the country through imported domestic animals and their ticks (Gofton 2018). Recent molecular microbiome profiling of native Australian ticks has produced preliminary evidence of novel *Ehrlichia* and *Anaplasma* in native soft and hard ticks feeding from humans (Gofton et al. 2015a), platypuses (*Ornithorhynchus anatinus*) (Gofton et al. 2018), short-beaked echidnas (*Tachyglossus aculeatus*), southern brown bandicoots (*Isodon obesulus*) (Egan et al. 2018) and cattle (Gofton 2018). The brown dog tick (*Rhipicephalus sanguineus*) transmits *Ehrlichia platys* to domestic dogs (*Canis familiaris*) in Australia (Brown et al. 2001). Its prevalence in domestic dogs is a significant threat to dingo (*Canis lupus dingo*) populations that have not had previous exposure, particularly if co-infection with multiple pathogens occurs (Smout et al. 2016). *Anaplasma* has an almost exclusive association with tick vectors and ruminant tick hosts; however, *Anaplasma bovis* has been detected in hard ticks parasitising bandicoots in Australia (Egan 2017), and other *Anaplasma* spp. are commonly responsible for disease in domestic dogs and cattle.

Members of the bacterial genus *Borrelia* can be categorised into those which cause two distinct clinical infections: Lyme borreliosis (LB) and tick-relapsing fever (RF). Lyme disease (caused by *Borrelia* spp. in the LB clade and transmitted by various species of *Ixodes* ticks) is highly prevalent overseas,

but has not yet been recognised or detected in ticks in Australia. Novel *Borrelia* spp. within the RF clade have been sequenced from hard ticks feeding on short-beaked echidnas (Loh et al. 2016) and a lace monitor (*Varanus varius*) (Panetta et al. 2017). *Rickettsia* spp. are well-known TBPs of humans and although both species of *Rickettsia*, which cause human disease in Australia, have been detected in native reservoir hosts, pathogenicity is yet to be described in native species (Graves and Stenos 2017). Ixodid ticks are considered ancestral arthropod hosts for *Rickettsia* spp. (Murray et al. 2016), with most tick-borne *Rickettsia* spp. belonging to the spotted-fever group and a few to the typhus group (Parola et al. 2005). *Rickettsia* spp. have been detected in Australian hard ticks parasitising Tasmanian devils (*Sarcophilus harrisi*) (Vilcins et al. 2009b), various reptiles (Stenos et al. 2003), bare-nosed wombats, short-beaked echidnas and koalas (*Phascolarctos cinereus*) (Vilcins et al. 2009c). The ornate kangaroo tick (*Amblyomma triguttatum*) is a three-host tick capable of colonising many host species and implicated in the spread of TBPs which cause disease in humans, including species of *Rickettsia* (Li et al. 2010). *Rickettsia* spp. are highly prevalent in many species of soft ticks parasitising wildlife outside Australia (Lafri et al. 2015; Yan et al. 2019); however, to date, the only *Rickettsia* spp. detected in Australian soft ticks have been collected from microbat dwellings (Tomassone et al. 2018).

The genus *Coxiella* (class, Gammaproteobacteria) is morphologically similar to *Rickettsia*; however, a range of genetic and physiological differences allow many members of this genus to persist in the environment for weeks to months (Koehler et al. 2019). The bacterial pathogen responsible for causing Q-fever (*Coxiella burnetii*) has been found in native ticks parasitising bare-nosed wombats (Vilcins et al. 2009c) and eastern grey kangaroos (*Macropus giganteus*) (Pope et al. 1960) and commonly harboured in livestock and cat reservoirs. Q-Fever is highly prevalent in Australia and of significant importance to those employed in the veterinary and agricultural industries. While the primary route of transmission for Q-fever is via aerosol, ticks play a major role in maintaining the pathogen and its life cycle within the environment (Maurin and Raoult 1999). *Francisella* is an additional genus of Gammaproteobacteria of note as a potential native TBP as it includes the known causative agent of the zoonotic disease tularaemia (Petersen et al. 2009). Novel species of *Francisella* have been isolated on two known occasions in Australia, including one from *Amblyomma fimbriatum* ticks parasitising various reptile species in the Northern Territory (Vilcins et al. 2009d), and again in *Amblyomma fimbriatum* parasitising Western Australian bobtail lizards (*Tiliqua rugosa*) (Mckenna 2019).

The genus *Wolbachia* is a known endosymbiont of ticks and nematodes associated with human disease (Pearlman et al. 2002) and has been detected in the oocytes of Australian hard

ticks parasitising reptiles (Stenos et al. 2003). Species in the bacterial order *Chlamydiales* are widely recognised for causing significant disease in humans and a variety of wild animals (Bodetti et al. 2003). They have been linked to tick and other arthropod vectors worldwide (Croxatto et al. 2014), and many novel species have been recently isolated in Australian ticks parasitising a range of marsupials and monotremes (Burnard et al. 2017). Candidatus *Midichloria mitochondrii* is a recently discovered endosymbiont of *Ixodes holocyclus* (Gofton et al. 2015b), with its discovery highlighting both the abundance of Australian tick endosymbionts and the ability of abundant symbionts to mask potentially medically important pathogens in 16S metabarcoding studies.

Protozoa

O'Donoghue and Adlard (2000) catalogued the protozoan parasites in Australia. Of these, only *Eimeria wombati*, *Eimeria ursini* and *Toxoplasma gondii* were described from the southern hairy-nosed wombat. *Eimeria arundeli*, *Eimeria* sp., *Toxoplasma gondii* and *Isothricha* sp. were described from the bare-nosed wombat.

Toxoplasmosis (caused by *Toxoplasma gondii*) is the most prevalent protozoan disease worldwide. Ixodid ticks from France, India, China and Poland (Gidel and Provost 1965; Singh et al. 1965; Sroka et al. 2009; Zhou et al. 2016) have tested positive for *T. gondii* and arthropod vectors have been proposed as an alternate route of transmission (Woke et al. 1953). Toxoplasmosis has been described as extremely prevalent in marsupials, including wild wombat populations (Donahoe et al. 2015)

Piroplasmids (*Babesia* and *Theileria* spp.) have been detected in hard ticks parasitising a range of marsupials. Species affected include northern quolls (*Dasyurus hallucatus*) (Obendorf 1993), common brushtail possums (*Trichosurus vulpecula*), western grey kangaroos (*Macropus fuliginosus*) (Loh et al. 2018b), eastern grey kangaroos, red-necked wallabies (*Macropus rufogriseus*), echidnas (Storey-Lewis et al. 2018) and long-nosed bandicoots (*Perameles nasuta*) (Loh et al. 2018a); however, they have not been detected in wombats.

Hepatozoon spp. are found in many arthropods and spread to mammals via the ingestion of an infected vector on a prey item or while grooming. They have been found in Australian ticks parasitising reptiles (Vilcins et al. 2009d) and Tasmanian devils (Vilcins et al. 2009b). Given their wide-ranging arthropod hosts, and their associated hosts, it is possible they may impact wombats and have not yet been detected. Furthermore, concerns for the biodiversity of Australian native fauna are warranted considering the devastating impacts seen in some populations overseas (Smith 1996).

Australia has a number of indigenous trypanosome species, some of which have been implicated in the decline of the

woylie (*Bettongia penicillata*) and western quoll (*Dasyurus geoffroyi*) (Cooper et al. 2018). The presence of trypanosomes has been detected in native Australian ticks and their vertebrate hosts (Barbosa et al. 2017), and while no experimental transmission studies have been conducted, ticks have long been speculated as vectors for Australian trypanosomes (Krige et al. 2019).

Viruses

Little is known about tick-borne viruses (also referred to as tiboviruses). Most tick-borne viruses that affect mammals appear to be associated with hard ticks (especially the genera *Ixodes*, *Dermacentor* and *Haemaphysalis*); however, the largest diversity of tick-borne viruses are in soft tick species which parasitise migratory birds (LaSala and Holbrook 2010). Some families of ticks have evolved to remain attached to their host for extended periods of time, which allows for long-distance travel, such as the genus *Hyalomma* of the family Ixodidae (Bjöersdorff et al. 2001). The Australian paralysis tick *I. holocyclus* has been suggested as a possible link between the transmission of Hendra virus between bats and horses (Barker 2003) and a novel virus (*I. holocyclus* ifavirus [IhIV]) was recently isolated from both engorged and unengorged field-captured *I. holocyclus* in Northern NSW and Queensland (O'Brien et al. 2018a). Furthermore, recent metatranscriptomic data have revealed the presence of novel species of Australian tick-borne viruses in native ticks which merit further investigation (Harvey et al. 2019).

Wombat ectoparasites

Host records appear to be the only current information available for most species; hence, seasonality and life cycles of ectoparasites which feed on wombats warrant further attention. Ectoparasite records of the northern hairy-nosed wombat (*Lasiorhinus krefftii*) are sparse due predominantly to the vulnerability of northern hairy-nosed wombats to extinction, making direct methods to examine both its parasite burden and the potential for those parasites to cause disease difficult (Gerhardt et al. 2000). Previous records include a minor “mange-like” skin condition only present in colder weather conditions, possibly caused by *S. scabiei* (Crossman 1988), the ornate kangaroo tick, the flea *Echidnophaga cornuta* and the louse *Boopis dubi* (Table 1) (Gerhardt et al. 2000). The ornate kangaroo tick is a three-host tick which primarily parasitises marsupials and macropods, and the other ectoparasites have only ever been associated with wombats.

Southern hairy-nosed wombat ectoparasite records include the fleas *Lycopsylla lasiorhini* (Mardon and Dunnet 1971), *E. octotricha*, *E. calabyi* (Dunnet and Mardon 1974) and *E. cornuta* (Doube 1981), the louse *B. dubia* (von Kéler

1971), the mite *S. scabiei* (Wells 1971) and dubious records of the wombat tick *Bothriocroton auruginans* (Roberts 1970). Some of these records predate existing abilities to distinguish southern-hairy nosed wombats and bare-nosed wombats, and as a result more records should be collected to confirm some of these host-parasite relationships (Barker and Walker 2014). It has been suggested that the flea *E. cornuta* is wombat specific, and until its discovery on northern hairy-nosed wombats it was thought, like *E. octotricha* and *E. calabyi*, to only parasitise southern hairy-nosed wombats (Dunnet and Mardon 1974). Another ectoparasite discovered to be shared only between northern and southern hairy-nosed wombats is the louse *B. dubia*. Given this louse has been associated with both host wombat populations, it provides further evidence that the distribution of these two wombat species likely once overlapped (Gerhardt et al. 2000). It also suggests that the genomes and microbial diversity of these shared ectoparasites may warrant comparison across host species.

Bare-nosed wombats are significantly impacted by the burrowing mite *S. scabiei*. The resulting sarcoptic mange has been relatively well studied as it is a significant disease of humans, domestic animals and other native mammals (Old et al. 2018; Skerratt 2001). The relationship between *S. scabiei* and other known wombat ectoparasites, their pathogens, ability to co-infect hosts and their overall impact on wombat hosts has not yet been investigated.

The mites *Acaroptes wombatus* (Skerratt 2001) and *Raillietia australis* (Skerratt 1998) have also been reported from bare-nosed wombats. The mite *A. wombatus* is endemic, regularly parasitises the skin surface of wombats and is not known to be associated with skin disease (Skerratt 1998). The ear mite *R. australis* has only been recorded on wombat hosts in south-eastern NSW and Victoria (Domrow 1987).

Other reported ectoparasites of bare-nosed wombats include the fleas *E. eyeri* and *L. nova* (Green 1993; Mardon and Allison 1978), with the latter species being described as a possible vector of wombat blood trypanosomes (Noyes et al. 1999). The bare-nosed wombat is the only confirmed host record for the louse *B. tarsata*, with an additional unconfirmed record from the swamp wallaby (*Wallabia bicolor*) (Werneck 1948). Unconfirmed reports of the fleas *E. perilis* and *E. myrmecobii* are likely to have been misidentified *E. calabyi* from southern hairy-nosed wombats (Dunnet and Mardon 1974).

Seven species of ticks have been collected from bare-nosed wombats including the wombat tick *B. auruginans* (Roberts 1953), wallaby tick *Haemaphysalis bancrofti* (Laan et al. 2011), Australian paralysis tick *I. holocyclus* (Jackson et al. 2007), southern paralysis tick *I. cornuatus* (Seddon 1968), *I. phascolomyis* (Macalister 1871), common marsupial tick *I. tasmani* and *I. victoriensis* (Roberts 1960). The tick *I. phascolomyis* is generally considered a *nomen dubium* as the description has been regarded inadequate (Roberts 1953).

Table 1 List of ectoparasite records for the three extant species of Australian wombats, and the pathogens associated with those tick species in Australia

Host species	Species	Type	Locality	Reference	Associated pathogens	Locality	Reference
Northern hairy-nosed wombat (<i>Lasiorhinus krefftii</i>)	<i>Amblyomma triguttatum</i>	Tick	Central QLD	(Gerhardt et al. 2000)	<i>Coxiella burnetii</i>	Western QLD	(Pope et al. 1960)
					<i>Rickettsia gravesii</i>	WA	(Owen et al. 2006)
					<i>Anaplasma bovis</i> genotype Y11	Yanchep NP and Barrow Island, WA	(Goffton et al. 2017)
					Ca. <i>Ehrlichia occidentalis</i>	Yanchep and Bungendore Park NPs, WA, SA and Innes NP, SA	(Goffton et al. 2017)
					<i>Ehrlichia</i> sp. and <i>Francisella</i> sp.	Torrens Basin, SA and Bowen, QLD	(Krige 2017)
Southern hairy-nosed wombat (<i>Lasiorhinus latifrons</i>)					<i>Anaplasma</i> sp.	Yanchep NP, WA	(Goffton et al. 2015a)
					<i>Ehrlichia</i> sp.	Bullsbrook, WA	(Goffton et al. 2015a)
					<i>Rickettsia</i> sp.	WA	(Goffton et al. 2015a)
	<i>Echidnophaga cornuta</i>	Flea	Central QLD	(Gerhardt et al. 2000)	None known	N/A	N/A
	<i>Boopis dubia</i>	Louse	Central QLD	(Gerhardt et al. 2000)	None known	N/A	N/A
	<i>Bothriocroton auruginans</i>	Tick		(Roberts 1970)	<i>Coxiella burnetii</i> and <i>Rickettsia massiliae</i>	Buxton, VIC	(Vilcins et al. 2009c)
	<i>Lycoposylla lasiorhini</i>	Flea	Yorke Peninsula, SA	(Dunnet and Mardon 1974; Mardon and Dunnet 1971)	None known	N/A	N/A
<i>E. octotricha</i>	Flea	Swan Reach, SA	(Dunnet and Mardon 1974)	None known	N/A	N/A	
<i>E. calabyi</i>	Flea	Sedan, SA	(Dunnet and Mardon 1974)	None known	N/A	N/A	
<i>E. cornuta</i>	Flea	Blanchetown, SA	(Doube 1981; Dunnet and Mardon 1974)	None known	N/A	N/A	
<i>B. dubia</i>	Louse	SA	(von Kéler 1971)	None known	N/A	N/A	
<i>Sarcoptes scabiei</i>	Mite	SA	(Wells 1971)	None known	N/A	N/A	
Bare-nosed wombat (<i>Vombatus ursinus</i>)	<i>Bothriocroton auruginans</i>	Tick	NSW, Vic, SA, Northern Tas, Flinders Island	(Roberts 1953)	<i>Coxiella burnetii</i> and <i>Rickettsia massiliae</i>	Buxton, VIC	(Vilcins et al. 2009c)
	<i>Haemaphysalis bancrofti</i>	Tick	Nadgee State Forest, NSW	(Laan et al. 2011)	<i>Theileria orientalis</i>	NSW, Vic, WA, SA	(Eamens et al. 2013; Islam et al. 2011)
					<i>Rickettsia felis</i> and <i>Coxiella burnetii</i>	Rockhampton Gladstone & Currumbin, QLD, Mollymook and Tamban, NSW	(Chalada et al. 2018)
					<i>Hepatozoon ewingi</i>	Eungai Creek, NSW	(Goffton et al. 2015a)

Table 1 (continued)

Host species	Species	Type	Locality	Reference	Associated pathogens	Locality	Reference
<i>Ixodes holocyclus</i>	<i>Ixodes holocyclus</i>	Tick	East Gippsland, Vic; Buccleuch State Forest, NSW	(Jackson et al. 2007)	<i>Coxiella burnetii</i> <i>Rickettsia australis</i> <i>Borrelia</i> sp., <i>Bartonella henselae</i> , <i>Ca. Neohhrlichia</i> spp., <i>Clostridium histolyticum</i> , <i>Rickettsia</i> spp., and <i>Leptospira inadai</i> <i>Rickettsia</i> sp. and <i>Ca. Neohhrlichia</i> sp. <i>Ehrlichia</i> sp. <i>Ca. Neohhrlichia australis</i> and <i>Ca. Neohhrlichia arcana</i> <i>Hepatozoon canis</i> and <i>Babesia lohae</i> <i>Ixodes holocyclus</i> ifavirus (IhIV)	Northern QLD Southeastern QLD NSW QLD, NSW, Vic Pimpama, QLD NSW and QLD Park Ridge, QLD Northern NSW and QLD	(Grey et al. 2018b) (Chalada et al. 2018; Cooper et al. 2013) (Campbell and Domrow 1974) (Goffton et al. 2015b) (Goffton et al. 2015a) (Goffton et al. 2015a) (Goffton et al. 2016) (Grey et al. 2018b) (O'Brien et al. 2018a) (Graves et al. 1993)
<i>I. cornuatus</i>	<i>I. cornuatus</i>	Tick	East Gippsland and Healesville, Vic	(Jackson et al. 2007; Seddon 1968; Skerratt et al. 2004)	<i>Rickettsia</i> sp. (SFG)	Gippsland, Vic	(Graves et al. 1993)
<i>I. phascolomyia</i> *	<i>I. phascolomyia</i> *	Tick	Unknown location in Aus—specimen in Dublin Zoological Gardens	(Macalister 1871)	None known	N/A	N/A
<i>I. tasmani</i>	<i>I. tasmani</i>	Tick	Gretna, Tas; Cooma and Buccleuch State Forest, NSW	(Roberts 1960; Skerratt et al. 2004)	<i>Rickettsiella</i> sp. <i>Rickettsia australis</i> <i>Bartonella</i> sp. <i>Theileria apogeana</i> , <i>T. palmeri</i> , <i>T. paparinii</i> , <i>T. worthingtonorum</i> , <i>Sarcocystidae</i> sp. and <i>Hepatozoon banethi</i> <i>Hepatozoon</i> sp. <i>Toxoplasma gondii</i> <i>Rickettsia</i> sp. (SFG) <i>Hepatozoon</i> sp. and <i>Rickettsia</i> sp. (SFG) <i>Rickettsia tasmanensis</i> <i>Theileria peramelis</i>	Phillip Island, Vic Southeastern QLD Phillip Island, Vic Tas Devonport and Port Sorell, Tas Seaforth, NSW Port Macquarie, NSW Tas Tas COET	(Vilcins et al. 2009c) (Campbell and Domrow 1974) (Vilcins et al. 2009a) (Grey et al. 2018b) (Grey et al. 2017) (Grey et al. 2017) (Vilcins et al. 2008) (Vilcins et al. 2009b)

Table 1 (continued)

Host species	Species	Type	Locality	Reference	Associated pathogens	Locality	Reference
	<i>I. victoricensis</i>	Tick	Healesville, Vic	(Roberts 1960; Skerratt et al. 2004)	<i>Trypanosoma</i> spp.	Albany and Two Peoples Bay, WA	(Izzard et al. 2009) (Weilgama 1986) (Austen et al. 2011)
	<i>E. eyeri</i>	Flea	Bairnsdale, Vic; Mt. Schank and Adelaide, SA	(Dunnet and Mardon 1974; Skerratt 2001)	None known	N/A	N/A
	<i>L. nova</i>	Flea	Hampden, NSW; Padilpa, Vic	(Dunnet and Mardon 1974; Skerratt 2001; Skerratt et al. 2004)	None known	N/A	N/A
	<i>E. perilis</i> **	Flea	Swan Reach, SA	(Dunnet and Mardon 1974)	None known	N/A	N/A
	<i>E. mymecobit</i> **	Flea	Long Reach, SA	(Dunnet and Mardon 1974)	None known	N/A	N/A
	<i>B. tarsata</i>	Louse	Healesville and Padilpa, Vic, NSW, Tas	(Palma and Barker 1996; Skerratt 2001; Skerratt et al. 2004)	None known	N/A	N/A
	<i>Sarcoptes scabiei</i>	Mite	NSW, Vic, SA, Tas, Flinders Island	(Martin et al. 1998; Old et al. 2018; Skerratt 2001)	<i>Klebsiella</i> sp., <i>Streptococcus</i> sp. and <i>Staphylococcus</i> sp.	UQ Gatton Campus	(Swe et al. 2019)
	<i>Acaroptes vombatius</i>	Mite	Healesville and Padilpa, Vic	(Skerratt 2001; Skerratt et al. 2004)	None known	N/A	N/A
	<i>Railiella australis</i>	Earmite	Healesville, Vic	(Domrow 1961; Skerratt 1998)	None known	N/A	N/A

NP national park, SFG spotted fever group, COET capable of experimental transmission

* Is generally considered a *nomen dubium* as the description has been regarded inadequate

** Both host and parasite likely misidentified due to geographical location and morphological similarity to *E. calabyi*

Some of the tick species previously found on wombats are known to feed on humans or domestic animals, including *I. holocyclus*, *A. triguttatum* and *H. bancrofti*. Of these three species, the best studied is *I. holocyclus*, which is highly prevalent along the east coast of Australia, and causes frequent illness (Mayne et al. 2014). Dogs can also commonly acquire *B. auruginans* when investigating wombat burrows (Barker and Walker 2014), which is where engorged ticks will fall off to develop to the next stage of their life cycle (Sonenshine and Roe 2013). Most of the tick species previously found on wombats are considered ‘generalist’ in that they will feed on multiple host species and do not rely on their primary host for survival (Laan et al. 2011; Oliver 1989). Ticks additionally use non-host species, for transportation or feeding; however, these hosts are not required for development of the parasite (Estrada-Peña and Jongejan 1999). Further research needs to be conducted to determine the relationship between ticks and other ectoparasites including their respective pathogens.

Wombats coevolved with native tick species, and healthy bare-nosed wombats regularly carry large burdens of ticks. Ticks are commonly picked up while grazing on vegetation where ticks are questing. Questing height is a reflection of host specificity for certain ticks. For example, larvae and nymphs are often found at the base of vegetation where birds and small mammals will frequent, where adult ticks will climb longer lengths of vegetation to reach larger vertebrate hosts (Sonenshine and Roe 2013). They are usually found in high numbers on ventral surfaces of wombats, and ticks are typically less prevalent on wombats with clinical signs of sarcoptic mange (Skerratt 1998; Skerratt et al. 2004).

Availability of genomes allows for fast and accurate identification of both arthropods and their associated microbial species, as well as providing information related to their evolutionary history (Brayton et al. 2001). Four ticks known to parasitise wombats have had their entire mitochondrial genome characterised (Table 2) (*Amblyomma triguttatum*, *Haemaphysalis bancrofti*, *I. holocyclus* and *I. tasmani*). The remaining three known wombat tick species have only partial sequences available (*Bothriocroton auruginans*, *I. cornuatus* and *I. victoriensis*) (Evans 2018). Host mobility typically determines geneflow in wingless vectors such as ticks, so

population genetic studies can provide insights into the basic biology of native ticks, host specificity and their potential to spread pathogens (Araya-Anchetta et al. 2015).

Pathogens of ticks that parasitise wombats

The hard tick *Amblyomma triguttatum* has been found on a few individuals in the population of approximately 250 northern hairy-nosed wombats (Horsup 2018). It is a known vector of *Bacillus* spp. (Murrell et al. 2003), the causative agent for Q-fever *Coxiella burnetti* (Pope et al. 1960), and *Rickettsia gravesii*, a novel spotted fever group member (Li et al. 2010). *Coxiella burnetti* has additionally been found in *B. auruginans* taken from bare-nosed wombats, as well as a *Rickettsia* sp. closely related to *R. massiliae* which causes human disease (Vilcins et al. 2009c). These are the only pathogens to be detected in ticks taken from wombat hosts.

The Australian paralysis tick *I. holocyclus* has long been thought to have an evolutionary relationship with bandicoots (Bagnall and Doube 1975), but has a wide host range and has been recorded on 34 mammal species and seven bird species, including bare-nosed wombats (Barker and Walker 2014; Beard et al. 2020). While it is well known to cause signs of paralysis often leading to death in humans, birds, domestic and native eutherian hosts (Campbell et al. 2003), bandicoots and other native marsupials have previously been found with heavy adult *I. holocyclus* burdens without clinical signs of tick paralysis (Jones 1991). In addition to tick paralysis, *I. holocyclus* is also a known vector of *Rickettsia australis*, the bacterial agent which causes Queensland tick typhus in humans (Storer et al. 2003). In contrast, the southern paralysis tick *I. cornuatus*, which has been studied to a lesser degree than *I. holocyclus*, is thought to cause similar paralysis signs in its hosts (Barker and Walker 2014).

Ixodes tasmani parasitises a wide range of small to large native mammals and hosts a range of parasites as well as being a known vector of *T. peramelis* (Weilgama 1986) and *R. australis* (Campbell and Domrow 1974). A spotted fever group *Rickettsia* sp. (Vilcins et al. 2008), *R. tasmanensis*

Table 2 Current availability of rRNA genetic data for the tick species known to parasitise wombats

Tick species	COI	ITS2	12S	16S	Entire mitochondrial genome
<i>Amblyomma triguttatum</i>	✓	✓	✓	✓	✓
<i>Bothriocroton auruginans</i>	✓	✗	✗	✗	✗
<i>Haemaphysalis bancrofti</i>	✓	✓	✓	✓	✓
<i>Ixodes holocyclus</i>	✓	✓	✓	✓	✓
<i>I. cornuatus</i>	✓	✓	✗	✗	✗
<i>I. tasmani</i>	✓	✓	✓	✓	✓
<i>I. victoriensis</i>	✓	✗	✗	✗	✗

(Izzard et al. 2009) and novel *Rickettsia* sp. (Vilcins et al. 2009c), *Hepatozoon* sp. (Vilcins et al. 2009b) and *Bartonella* sp. (Vilcins et al. 2009a) have also all been isolated from *I. tasmani*. The filarioid nematode *Cercopithifilaria johnstoni* has been documented in *I. tasmani* during moulting and can be transmitted from one host to another (Spratt and Haycock 1988). Very little is known about the life cycle or pathogenicity of *I. victoriensis* and only a few specimens have ever been collected from bare-nosed wombat and potoroo (*Potorous tridactylus apicalis* and *P. longipes*) hosts (Weaver 2016). A *Trypanosoma* sp. with 99.9% homology to the wombat isolate of *T. copemani* was detected in *I. victoriensis* specimens from quokkas (*Setonix brachyurus*) and Gilbert's potoroos (*Potorous gilbertii*) (Austen et al. 2009). The authors of this study hypothesised that *I. victoriensis* is a natural vector for *Trypanosoma* spp. and that transmission may occur via ingestion of ticks and their faeces during grooming (Austen et al. 2009); however, due to their body structure, wombats exhibit a unique grooming method using their claws and objects in the environment to scratch their bodies rather than their teeth and mouth (Triggs 2009). This grooming style likely inhibits ingestion of ectoparasites and restricts pathogen acquisition to bites.

A bacterium associated with *S. scabiei* and mange infection in the Northern Hemisphere, *Corynebacterium* spp. (DeCandia and Leverett 2019; Swe et al. 2014) have also been isolated from the gastrointestinal tract of three tick species (*Ixodes ricinus*, *Dermacentor reticulatus* and *Haemaphysalis concinna*) (Rudolf et al. 2009). *Corynebacterium* spp. cause significant diseases in Australia primarily impacting sheep and humans (Paton et al. 1988; Peel et al. 1997); however, this bacterium has not been identified in any Australian ticks or mites. In addition, it has been found that mammals with sarcoptic mange consistently present with an altered and decreased skin microbiome which allows for opportunistic pathogens associated with arthropod vectors to cause infection (DeCandia and Leverett 2019). The relationship between sarcoptic mange infection and the pathogens in ticks and mites on wombats warrants further research.

Pathogens of other wombat ectoparasites

No species of lice that feed on wombats has been assessed for endosymbionts or potential pathogens. The flea *Echidnophaga myrmecobii* has doubtfully been recorded from a bare-nosed wombat (Dunnet and Mardon 1974) (Table 1). Two *Bartonella* spp. have been isolated from *E. myrmecobii* taken from cats and rabbits, in addition to other *Echidnophaga* spp. from native marsupials (Kaewmongkol et al. 2011). The mite *Acaroptes vombatus* has only been found on wombats (Skerratt 2005). Wombats with heavy infestations of *A. vombatus* can display similar clinical signs of scale and hair

loss to sarcoptic mange (Skerratt 2005). These results indicate the pathogenic potential of other native ectoparasites and should be investigated further.

The presence of several ectoparasite species is known to impact on health parameters of native marsupials such as possums (Webster et al. 2014) and bandicoots (Gemmell et al. 1991). The additional immunological burden of ticks, mites, fleas and their associated pathogens may play a role in the susceptibility of bare-nosed wombats to sarcoptic mange. In addition, the ability of ticks to acquire, harbour and possibly co-transmit multiple pathogens while co-feeding on the same vertebrate host has been shown (Moutailler et al. 2016; Richter et al. 2002), but this is not the case for other ectoparasite species. This lends possibility to *Sarcoptes* mites acquiring tick-associated pathogens. Zenskaya and Pchelkina (1967) showed that the poultry red mite (*Dermanyssus gallinae*) is able to acquire *C. burnetii* from an infected host while feeding. The same metabarcoding tools used to assess tick microbiomes can be applied to other types of ectoparasites, yet very few studies have utilised these modern tools for investigating the microbes of fleas, lice or mites.

Many species of fleas, lice and mites are considered vectors of pathogens to humans and animals overseas. Fleas are known as vectors of murine typhus (caused by *Rickettsia typhi*) (Henry et al. 2007), and play a role in the transmission of rural epidemic typhus (*Rickettsia prowazekii*) in the USA (WHO 1989). The European rabbit flea (*Spilopsyllus cuniculi*) is the main vector of myxomatosis in Britain (Mead-Briggs and Vaughan 1975). The mite, *Varroa destructor*, transmits pathogenic viruses to honeybees (Genersch et al. 2010; Highfield et al. 2009). Durden et al. (1992) have shown experimentally that Venezuelan Equine Encephalitis Virus (Togavirus) can be transmitted by *D. gallinae*, which has been implicated in the spread of *Salmonella* spp. causing avian salmonellosis in poultry facilities (Chirico et al. 2003; Moro et al. 2009). Thus, many studies have either isolated pathogens from mites, fleas and lice, or have successfully shown transmission of pathogens to their hosts. These ectoparasites have largely been ignored as potential vectors of disease compared to ticks and mosquitoes, and as a result very few studies have shown both isolation and transmission (Moro et al. 2009), which is required to consider an ectoparasite a vector of that pathogen.

Conclusions and further research

This review summarises the current information available on the ectoparasites that parasitise wombats, with a focus on ticks, as well as the pathogens associated with those ticks. Further research is required on the identification of entire bacterial communities within tick species, as well as protozoal and virus identification, determination of the pathogenicity of these microorganisms and their impact on both healthy and immunocompromised wombats. Wombats are

particularly vulnerable to the effects of ectoparasites as seen in their affliction to sarcoptic mange caused by the burrowing mite *Sarcoptes scabiei* (Skerratt 2001), leaving wombats immunocompromised and prone to secondary pathogenic infections (Old et al. 2018). However, ticks are responsible for the widest range of pathogens of any arthropod vector and studies of native tick species and their impacts on native species, including wombats, are limited. It is therefore critical to investigate more widely the impact of TBPs on native species, including wombats. Furthermore, while bare-nosed wombats are regarded as least concern on the IUCN Red List of Threatened Species (Taggart et al. 2016b), the southern hairy-nosed wombats are listed as near-threatened (Woinarski and Burbidge 2016) and northern hairy-nosed wombats are listed as critically endangered (Taggart et al. 2016a); hence, the roles of parasites and pathogens that impact these species are required to ensure continued conservation of all wombats.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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