



Invited Review

Diversity in parasitic helminths of Australasian marsupials and monotremes: a molecular perspective



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ABSTRACT

Marsupials and monotremes are a prominent part of the mammalian fauna in Australia, and harbour an extremely diverse and highly distinctive array of helminth parasites. Their study has been relatively neglected, likely because they have no direct, adverse socioeconomic impact. As the body plans of helminths generally are very simple and morphological characterisation likely underestimates true diversity, molecular tools have been employed to assess genetic diversity. Using biochemical and/or molecular methods, recent studies show extensive diversity in helminths of marsupials, with cryptic species being commonly encountered. The purpose of this article is to review current knowledge about the diversity of parasitic helminths of marsupials and monotremes, to raise questions as to whether current molecular data can be used to estimate diversity, what mechanisms lead to such diversity, to critically appraise the molecular tools that have been employed thus far to explore diversity and to discuss the directions which might be taken in the future employing improved techniques.

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1. Introduction

Marsupials and monotremes constitute a prominent component of the Australasian mammalian fauna, and harbour an extremely diverse and highly distinctive array of helminth parasites (Spratt et al., 1991; Beveridge and Spratt, 1996). Most are host specific and do not infect domestic livestock (although the common parasites of livestock, *Echinococcus granulosus*, *Fasciola hepatica* and *Trichostrongylus* spp., readily infect several species of marsupials). This lack of economic significance may well be a reason as to why their study has been relatively neglected. Some species, such as the trichostrongyloid nematode *Globocephaloides trifidospicularis*, can cause significant disease, including mortalities, in free ranging kangaroo hosts (Arundel et al., 1990), while species of *Strongyloides* (undescribed) cause mortality in captive kangaroos (Winter, 1958). However, the pathogenicity of most species and their life cycles remain to be determined.

In 1909 in Sydney, Australia, T.H. Johnston and J.B. Cleland (1909), both subsequently professors at the University of Adelaide, Australia, set out to document the parasitic fauna of Australian mammals. In spite of their valiant efforts and those of their students, particularly J.M. Mackerras, P.M. Mawson, L.M. Angel and S.J. Edmonds, much remains to be done (Spratt et al., 1991).

Numerous helminth species in museum collections remain to be described, and numerous species of marsupial remain to be examined for parasites. In spite of obvious difficulties, a substantial body of information on the helminth parasites of marsupials and monotremes has been accumulated (see Mackerras, 1958; Beveridge and Spratt, 1996) since Johnston and Cleland stated their aim of documenting the fauna. Currently, two features of the helminth fauna of Australasian marsupials and monotremes, as currently understood, stand out: their diversity and their phylogenetic associations. The diversity of these parasites of marsupials and monotremes is reviewed here in the light of recent publications on molecular aspects of this topic.

The Australasian realm is well recognised as being highly biodiverse with a very significant degree of endemism. While generally appreciated with respect to plants, vertebrates and the more conspicuous groups of invertebrates (such as insects), there appears to be little understanding that the same principles apply to helminth parasites. Current data (Spratt et al., 1991) suggest that the diverse helminth fauna in marsupials is indeed largely endemic, as might be expected.

The diversity of helminths among the various marsupial groups is not uniform, with the Dasyuromorpha (dasyurids) and Peramelemorpha (bandicoots) (basal taxa) exhibiting high parasite diversity, while the intermediate diprotodont clades Vombatoidea (koalas and wombats), Phalangerioidea (possums and cuscuses) and the early macropodoid clades containing the rat-kangaroos

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(Hypsiprymnodontidae and Potoroidae) show limited parasite diversity, possibly attributable to the arboreal or fungivorous habits of most of their representatives. By contrast, the most extreme diversity occurs in the herbivorous Macropodidae (kangaroos and wallabies) (Beveridge and Spratt, 1996), with 372 species of helminths recorded to date (Beveridge et al., 2010). The diversity of cloacinine nematodes in kangaroos and wallabies exceeds that of any other known group in mammals (Beveridge and Chilton, 2001).

Current estimates of parasite diversity need to be viewed with some degree of caution. To date, there are records of parasites from 145 of the 227 known species of marsupial (82 species have never been examined for parasites) and many of the species for which there are records have been examined in small numbers only. The data suggest that the dasyurids (Dasyuridae) and the possums (Petauridae and Phalangeridae) are the families in which the major deficits in our knowledge remain to be addressed.

In addition, even in the commonly encountered species of kangaroos and wallabies, due to the large numbers of nematodes present in the sacculated forestomachs (tens of thousands), less common species may be readily overlooked (Vendl and Beveridge, 2014). For these many reasons, it is evident that even the current, high diversity of helminths present in Australasian marsupials probably represents a gross underestimate of true diversity.

2. Molecular studies

It has long been recognised that the body plans of helminths generally are very simple and that morphological characterisations may represent a significant underestimate of true diversity. Recent applications of biochemical and molecular methods have confirmed this general hypothesis, particularly with respect to the helminths of marsupials. Several taxa have been identified to include cryptic species. The definition of a cryptic species adopted here is that of Bickford et al. (2007) as 'two or more species which are currently hidden under one species name'. The terms 'sibling species' or 'sister species' (as used by Bickford et al., 2007) have been avoided as they imply the establishment of phylogenetic relationships which are generally not applicable to the studies described here (see also Nadler and Pérez-Ponce de León, 2011).

2.1. Cloacinine and phascolostromyline nematodes

The cloacinine nematodes (order Strongylida, family Chabertiidae) found in the gastrointestinal tracts (oesophagus and stomach) of kangaroos and wallabies are the most speciose sub-family of nematodes known from mammals (Beveridge and Chilton, 2001). Initial biochemical studies of this group of nematodes used multilocus enzyme electrophoretic (MEE) analyses (Andrews and Chilton, 1999) and targeted instances of morphologically variable nematode species occurring in different hosts. The outcomes were consistent and in each instance where morphological variability was noted, biochemical and therefore genetic evidence was obtained to support the existence of separate species.

Several studies were undertaken within the genus *Rugopharynx* (Chilton et al., 1993a; Beveridge et al., 1994), each revealing pairs of cryptic species. The largest group studied was the *Rugopharynx australis* complex, one of the commonest 'species' found in the stomachs of kangaroos and wallabies. An MEE study of this species indicated the existence of seven distinct genetic groups (Chilton et al., 1996) and a subsequent morphological study resulted in the description of nine new species and the resurrection of a tenth species (*Rugopharynx alpha*) within this complex (Beveridge and Chilton, 1999). Subsequent DNA sequence studies have supported the original allozyme data (N.B. Chilton and I. Beveridge,

unpublished data) and suggest that additional species remain to be described within the complex. All species described within this complex can now be recognised morphologically, in some cases by relatively minor characters such as the extremely slender externo-dorsal ray in *Rugopharynx mu* and the differing position of the nerve ring (anterior to the oesophageal isthmus) in *Rugopharynx rho* (Beveridge and Chilton, 1999), characters which had been overlooked in previous studies. Beveridge (1982) had suggested that *R. australis* was a species complex, but had concluded that the morphological characters available at the time were insufficient to allow the description of new species.

Hypodontus macropi is a hookworm-like strongyloid (family Chabertiidae, sub-family Phascolostromylinae) occurring in the ileum, caecum and colon of various species of kangaroos and wallabies (Beveridge, 1979a). Inconsistencies in its host distribution led to the hypothesis that it represented a series of host-specific, cryptic species. Evidence in support of this hypothesis was provided initially by an MEE study (Chilton et al., 1992a) and was further supported by DNA sequence data (Chilton et al., 1995, 2012), suggesting that *H. macropi* is a complex of at least 10 species. However, this evidence was based exclusively on sequence data for the second internal transcribed spacer (ITS-2) of nuclear ribosomal DNA. As has been pointed out (Criscione et al., 2005; Nadler and Pérez-Ponce de León, 2011), this level of investigation represents 'molecular prospecting', providing evidence for the potential existence of sibling species, but is not definitive evidence that the genetically distinct groups detected represent species. In this instance, additional evidence is available from a mitochondrial genomic study of several component taxa (Jabbar et al., 2013), thereby strongly supporting the case for the existence of distinct, genetic species. Detailed morphological studies are required to ascertain whether or not these species are recognisable morphologically.

Cloacina is the most speciose genus of the cloacinine nematodes found in macropodid marsupials, with 110 species currently described (Beveridge, 1998, 1999, 2002; Beveridge and Speare, 1999). The occurrence of cryptic species within this large genus was initially indicated in MEE studies of *Cloacina petrogale* (see Chilton et al., 1997a), which resulted in the description of four species within this complex (Beveridge, 1998).

Rock wallabies (*Petrogale* spp.) occur as relatively isolated populations on rocky habitats throughout Australia. Along the north-eastern coast of the continent, a series of parapatric species of rock wallabies belonging to the *Petrogale penicillata* complex occurs, intermixed with *Petrogale persephone*, a more primitive rain forest-dwelling species (van Dyck and Strachan, 2008). These hosts share several species of the nematode genus *Cloacina* which occur exclusively in rock wallabies. Analysis of *Cloacina caenis*, *Cloacina pearsoni* and *Cloacina robertsi* from various hosts using markers in the internal transcribed spacers (ITS = ITS-1 and ITS-2) suggested that there were genetic differences in the nematodes from each species of rock wallaby (Chilton et al., 2009a). As the extent of sequence differences in ITS used to delimit new species is controversial, Chilton et al. (2009a) used the concept of autapomorphic sites, proposed by Adams (1998) and Nadler et al. (2000), to support their hypothesis that the genetic differences detected may represent different species. If current hypotheses prove to be corroborated by more extensive sequencing, the initial three species investigated may be represented by 15 species.

The above studies targeted taxa occurring in multiple host species. An alternative approach was taken by Tan et al. (2012), who examined the case of a disjunct distribution of a parasitic nematode, *Macropoanema comani* is a common parasite of eastern grey kangaroos (*Macropus giganteus*) along the eastern coast of Australia and, hence, the finding of morphologically similar specimens in the northern wallaroo (*Macropus robustus woodwardi*) in the Northern

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