Systematic Parasitology **32**: 149–156, 1995.

Relationships within the *Rugopharynx delta* species complex (Nematoda: Strongyloidea) from Australian marsupials inferred from allozyme electrophoretic data

I. Beveridge, N.B. Chilton[2,4] and R.H. Andrews[3]
[1]*Department of Veterinary Science, University of Melbourne, Parkville, Victoria 3052, Australia*
[2]*Evolutionary Biology Unit, South Australian Museum, Adelaide, SA, Australia*
[3]*Department of Microbiology & Immunology, University of Adelaide, SA, Australia*
[4]*Present address: Department of Veterinary Science, University of Melbourne, Parkville, Victoria, Australia*

Accepted for publication 19th October, 1994

Abstract

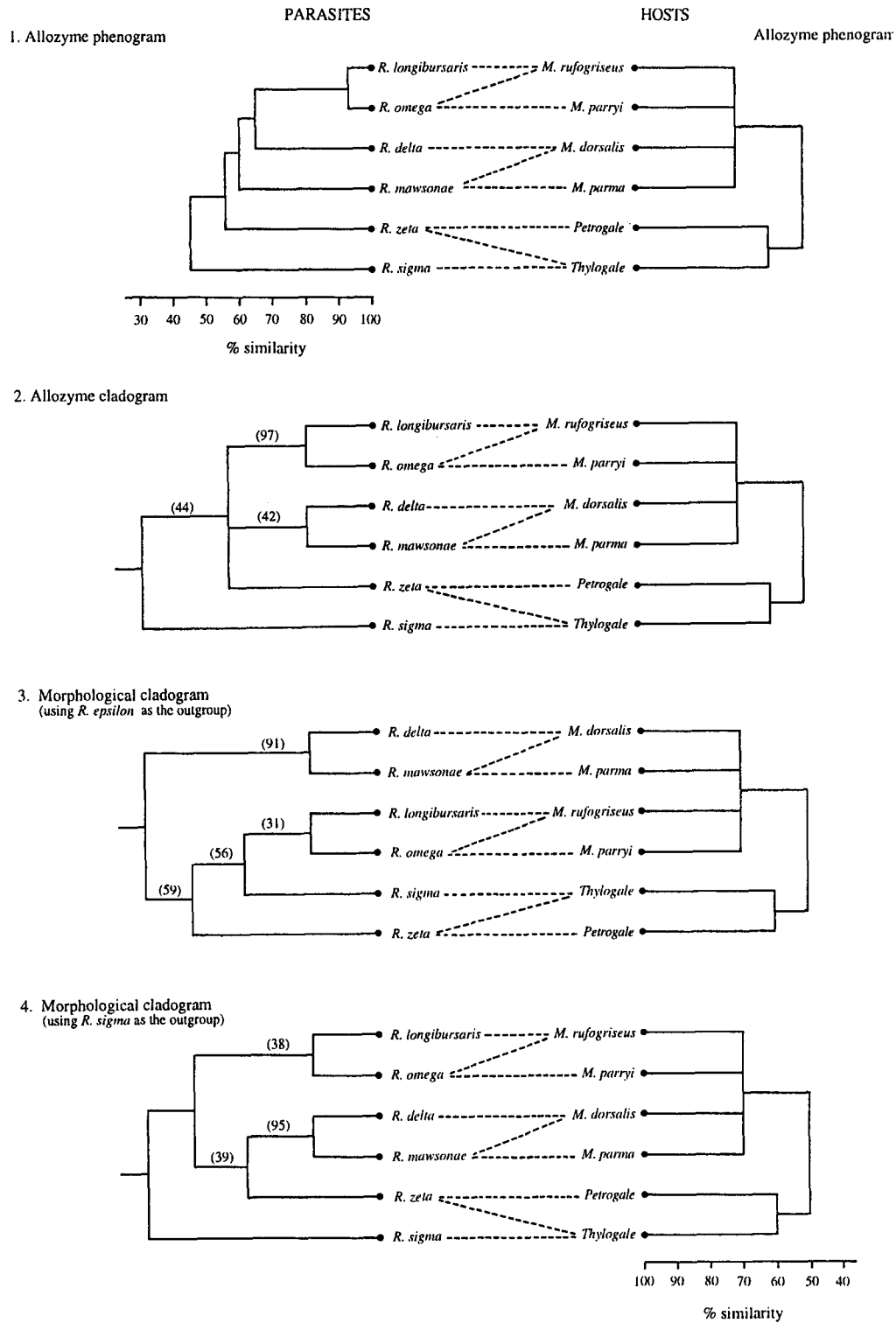
Relationships between the strongyloid nematodes *Rugopharynx delta*, *R. zeta*, *R. omega*, *R. longibursaris*, *R. mawsonae* and *R. sigma*, all from macropodid marsupials, were investigated using allozyme data. The phylogenetic trees derived from the electrophoretic data set were congruent with those of the hosts and were consistent with the hypothesis that the species complex originated in pademelons of the genus *Thylogale* and diversified in rock-wallabies (*Petrogale* spp.) and scrub wallabies of the subgenus *Notamacropus*. Host switching is evident only between closely related macropodid taxa.

Introduction

Species of the strongyloid genus *Rugopharynx* Mönnig, 1927 are prominent members of the diverse nematode fauna occurring in the stomachs of kangaroos and wallabies of the genera *Macropus*, *Wallabia*, *Petrogale* and *Thylogale* (see Beveridge, 1982). A major species complex within the genus, characterised by a trilobed buccal capsule, is the "*Rugopharynx delta* complex", based on the first named species, *R. delta* (Johnston & Mawson, 1939). Apart from *R. delta*, two additional species, *R. zeta* (Johnston & Mawson, 1939) and *R. longibursaris* (Kung, 1948) were considered valid by Beveridge (1982), who also added *R. omega* Beveridge, 1982. This latter species was distinguished from *R. longibursaris* only by the morphology of the spicule tip. Beveridge (1982) also noted that the morphological features of *R. zeta* were highly variable and suggested that it might constitute a species complex. A subsequent electrophoretic study of *R. zeta* from rock-wallabies (*Petrogale* spp.) and scrub-wallabies (*Macropus* spp.) revealed the existence of an additional species, *R. mawsonae* Chilton, Beveridge & Andrews, 1994 present in *Macropus* spp. A comparable examination of *R. omega* and *R. longibursaris*, both from *Macropus rufogriseus*, found few electrophoretic differences between them, but did reveal the existence of a cryptic species within *R. omega*, which was described and named *R. sigma* Beveridge, Chilton & Andrews, 1993. It is restricted to pademelons, *Thylogale* spp. (Table I).

Electrophoretic differences between *R. zeta* and *R. mawsonae* were of a similar magnitude to those found when each was compared with the morphologically distinct *R. delta* (see Beveridge *et al.*, 1994). In the case of *R. omega* and *R. sigma*, which are difficult to distinguish morphologically, fixed genetic differences were detected at 45% of the 20 enzyme loci examined (Chilton *et al.*, 1993). This suggests that there may be little correlation between morphological and electrophoretic differences.

Based on morphological and electrophoretic data sets, tentative proposals have been suggested for the evolution of the *R. omega* – *R. longibursaris* species pair in *Macropus rufogriseus* (see Chilton *et al.*, 1993) and *R. zeta* – *R. mawsonae* in *Petrogale* spp. and *Macropus* spp. (see Beveridge *et al.*, 1989; Beveridge *et al.*, 1994). These suggestions need to be tested against a working hypothesis for the evolution of the entire *R. delta* complex.


PARASITES
HOSTS
1. Allozyme phenogram
Allozyme phenogram
R. longibursaris
R. omega
R. delta
R. mawsonae
R. zeta
R. sigma
M. rufogriseus
M. parryi
M. dorsalis
M. parma
Petrogale
Thylogale
30 40 50 60 70 80 90 100
% similarity
2. Allozyme cladogram
(97)
(44)
(42)
3. Morphological cladogram
(using R. epsilon as the outgroup)
(91)
(31)
(56)
(59)
4. Morphological cladogram
(using R. sigma as the outgroup)
(38)
(95)
(39)
100 90 80 70 60 50 40
% similarity

In this paper, we examine the electrophoretic data of Beveridge *et al.* (1994) and Chilton *et al.* (1993) to determine the extent to which they indicate evolutionary relationships within the *R. delta* complex.

Materials and methods

Electrophoretic data

Data derived from studies by Beveridge *et al.* (1994) and Chilton *et al.* (1993) were combined and alleles scored depending upon relative mobility (Table II). For some enzyme loci, the samples were re-examined electrophoretically to confirm the relative mobility of bands. As a result, the alleles expressed by *R. zeta* for *Gda* were established. Some scorings therefore differ from those found in the original papers cited. The data for *Pgm* were not included in the present study because we were unable to determine unequivocally whether the *Pgm* locus in *R. zeta* and *R.mawsonae* corresponds with *Pgm-1* or *Pgm-2* in *R. sigma, R. longiburaris* and *R. omega*. Phenetic relationships were determined from fixed genetic differences analysed by the UPGMA method (Sneath & Sokal, 1973).

Cladistic analysis of electrophoretic data is controversial (for summaries see Gardner, 1991, Barker *et al.* 1992, Georges & Adams, 1992). Here, loci were used as characters and alleles as unordered character states (see Barker *et al.*, 1992). Loci were scored numerically according to increasing mobility from the cathode (Table IV). Treatment of polymorphisms followed the methods of Georges & Adams (1992). Unique alleles and complex allele patterns were ignored. *R. epsilon* and *R. australis* were initially considered as outgroups. The adult stage of *R. epsilon* has a bilobed buccal capsule; however, the fourth larval stages of both *R. zeta* and *R. epsilon* have simple, cylindrical buccal capsules resembling the adult of *R. australis* (Mönnig, 1926) and *R. theta* (Johnston & Mawson, 1939). Hence the species with cylindrical buccal capsules are considered to represent the plesiomorphic state. Both *R. australis* and *R. epsilon* were therefore included as potential outgroups. However, when electrophoretically compared with members of the *R. delta* complex, they had fixed differences exceeding 80% and were therefore not considered suitable as outgroups for phylogenetic analysis. Phylogenetic trees produced by PAUP were instead rooted with *R. sigma* as an outgroup, identified from the phenetic analysis as the most distantly related member of the complex, or using a hypothetical outgroup (i.e. with all character states plesiomorphic). Data were analysed using PAUP version 3.0s (Swofford, 1992) and equally parsimonious trees presented as the 50% consensus tree. The numbers of trees with a particular branch were determined using the Bootstrap option in PAUP, based on 100 trees.

Morphological data

Morphological characters were obtained for the various species of the *R. delta* complex (Table I) from Beveridge (1982), Beveridge *et al.* (1994) and Chilton *et al.* (1993) (Table III). Continuous (metric) characters (spicule length, tail length) were examined by plotting the mean length of the organ or body part against total body length and identifying clearly separate groups of species. Polarity of characters was determined by the outgroup method (Wiley, 1981). For these analyses, two outgroups were selected. In our analysis, *R. sigma* was used as the outgroup, since it had been used for the same purpose in the electrophoretic analysis. In another analysis, *R. epsilon*, originally selected as an outgroup for analysis of the electrophoretic data, was used in an analysis of the morphological data (Table V). Bootstrap analyses were performed on the resultant consensus trees.

Host data

Parasite trees were compared with host derived from the electrophoretic data of Richadson & McDermid (1978) and Baverstock *et al.* (1985). Since these two data sets differ in methods of analysis and in component species, a composite of both sets has been utilised here. Because of deficiencies in the host data, detailed host-parasite comparisons (e.g. Gardner, 1991; Page 1991) were not possible.

Figs 1–4. Nematode parasite and host relationships for members of the *Rugopharynx delta* complex, occurring in *Macropus, Thylogale* and *Petrogale*. 1. Parasite relationships based on phenetic (UPGMA) analysis of allozyme data. 2. Parasite relationships based on cladistic analysis of allozyme data. 3. Cladistic analysis based on morphological data using *R. epsilon* as the outgroup. 4. Cladistic analysis of morphological data using *R. sigma* as the outgroup. Host trees are phenograms based on data in Richardson & McDermid (1978). Figures in parentheses indicate percentage occurrence of a particular configuration in bootstrap analyses. Oblique lines indicate instances of host switching.

Table I. Component species of the *Rugopharynx delta* complex, their hosts are known geographical ranges.

Nematode	Host(s)	Distribution
R. delta	*Macropus (Notamacropus) dorsalis**	Eastern Queensland
R. mawsonae	*M. (N.) dorsalis**, *M. (N.) parma*	Eastern Queensland, north eastern New South Wales
R. zeta	*Petrogale assimilis**, *P. mareeba*†, *P. sharmani*†, *P. inornata*, *P. herberti*†, *P. penicillata*, *Thylogale thetis*	Eastern Queensland, north-eastern New South Wales
R. longibursaris	*M. (N.) rufogriseus**	Tasmania, western Victoria, south-eastern South Australia
R. omega	*M. (N.) rufogriseus**, *M. (N.) parryi*	South-eastern Queensland, eastern New South Wales, eastern Victoria
R. sigma	*Thylogale stigmatica**, *T. calabyi*	North-eastern Queensland, Papua-New Guinea
R. ? cf. *omega*	*T. thetis*	South-eastern Queensland.

*Indicates hosts from which nematodes have been examined electrophoretically.
† Host nomenclature following Eldridge & Close (1992).

Results

Electrophoretic data

Phenetic analysis of the electrophoretic data resulted in a tree with *R. sigma* on the outermost branch, followed by *R. zeta*, *R. mawsonae* and *R. delta* on the inner branches. *R. omega* and *R. longibursaris* were the most similar (Fig. 1).

In the cladistic analysis of the allozyme data (Fig. 2), the enzyme loci *Acon, Ak, Hex, Idh, Pgam* and *Ugpp* were eliminated because they were uninformative. The analysis, rooted on *R. sigma*, examined 105 trees and produced four equally parsimonious trees; and 50% majority rule consensus tree had a length of 31 and a consistency index of 0.69. Nine trees had a total length of 32 each. When rooted using a hypothetical ancestor as an outgroup, a tree with an identical topology to that of the first tree resulted. *R. omega* and *R. longibursaris* were associated in 97% of trees, while asociations between other taxa occured in fewer than 50% of trees (Fig. 2). The allozyme phenogram and cladogram were similar in that *R. omega* and *R. longibursaris* were closely associated. *R. delta* and *R. mawsonae* were closely associated in the cladogram and the phenogram, but were not necessarily nested together.

Morphological data

Using *R. sigma* as the outgroup, a single most parsimonious tree of 945 was obtained with a length of 14 and a consistency index, following the exclusion of uninformative characters, of 0.73. Three additional trees each had lengths of 15. The topology (Fig. 3) was virtually identical to that of the allozyme cladogram with *R. longibursaris* – *R. omega* and *R. delta* – *R. mawsonae* nested with *R. zeta*. Using *R. epsilon* as the outgroup, a tree with a different topology was obtained (Fig. 4), based on the consensus of 2 equally parsimonious trees. The tree length was 14 and the consistency index 0.73. Twelve trees each had a total length of 15.

Discussion

The phenogram and cladogram based on parasite allozyme data were similar in topology. Differences included the nesting of *R. delta* and *R. mawsonae* in the cladogram, but not in the phenogram and the position of *R. zeta* as the sister group to *R. omega* – *R. longibursaris* – *R. delta* – *R. mawsonae* in the phenogram, compared with the trichotomy *R. zeta*, *R. delta* – *R. mawsonae* and *R. omega* – *R. longibursaris*

Table II. Allelic profiles for members of the *Rugopharynx delta* species complex.

	Acon	*Ald*	*Ak*	*Cs*	*Enol*	*Est*	*Gda*	*Gdh*	*Got*	*Gpi*	*Gpt*	*Gsr*	*Hex*	*Idh*	*Mdh*	*Mpi*	*Ndpk*	*PepA*	*PepC*	*Pgam*	*Tpi*	*Ugpp*
R. zeta	a*	b*	a	b	a	bc	a	b	a	c	c	b	a	a	b	–	b	c	a	d	a	a
R. mawsonae	a	b	ab	b	bc	cd	cd	a	c	c	b	a	a	a	b	–	b	b	b	c	b	a
R. delta	a	b	a	a	b	b	bc	b	b	bc	a	a	a	a	b	–	ab	a	a	ab	b	a
R. omega	–	b	a	b	b	bc	c	b	b	c	b	c	a	a	a	ab	a	e	b	bd	a	a
R. sigma	–	a	a	a	b	a	b	a	b	a	b	c	a	b	–	a	b	c	–	b	a	a
R. longibursaris	–	b	a	b	b	bc	c	b	b	c	b	c	a	a	a	ab	a	df	b	bd	a	a

* Alleles scored according to increasing mobility from the cathode.

Abbreviations from enzyme loci: *Acon*, Aconitase; *Ald*, Aldolase; *Ak*, Adenylate kinase; *Cs*, Citrate synthease; *Enol*, Enolase; *Est*, Esterase; *Gda*, Guanine deaminase; *Gdh*, glutamate dehydrogenase; *Got*, Aspartate aminotransferase; *Gpi*, Glucose phosphate isomerase; *Gpt*, alanine aminotransferase; *Gsr*, glutathione reductase; *Hex*, Hexosaminidase; *Idh*, Isocitrate dehydrogenase; *Mdh*, Malate dehydrogenase; *Mpi*, Mannose-phosphate isomerase; *Ndpk*, Nucleoside diphosphate kinase; *PepA*, Peptidase valine-leucine; *PepC*, Peptidase lysine-leucine; *Pgam*, Phosphoglyccrate mutase; *Tpi*, Triosephosphate isomerase; *Ugpp*, UTP-glucose-1-phosphate uridyltransferase. Enzyme Commission (E.C.) number for each enzyme given in Beveridge *et al.* (1993b) and Chilton *et al.* (1993).

in the cladogram. These differences were considered to be relatively minor. Such differences might arise from the different type of analysis used, particularly since several enzymes used in the phenetic analysis were uninformative in a cladistic sense and were therefore excluded from the cladistic analysis. Cladograms and phenograms resemble one another when evolutionary rates are approximately the same in all taxa, and such congruence has been reported in electrophoretic studies of the related strongyloid nematode genera *Hypodontus* and *Macropostrongyloides* (see Chilton *et al.*, 1992, Beveridge *et al.*, 1993).

The trees based on morphological characters differed significantly depending on the outgroup utilised. The tree utilising *R. sigma* as an outgroup produced a cladogram similar to that derived from the electrophoretic data, utilising the same outgroup. However, when *R. epsilon* was used as the outgroup, a use fully justifiable on the basis of morphology, a tree of quite different topology was produced. A potential source of differences in tree topology can be due to tree rooting. Barker *et al.* (1992) in an electrophoretic study of the lice (Phthiraptera) of rock wallabies (*Petrogale* spp.) found that different outgroups produced trees of markedly different topologies. They attributed this to some outgroups being too distant from the ingroup analysed. In the current study, *R. epsilon*, selected on morphological grounds as being a suitable outgroup, proved to be too different electrophoretically for cladistic analysis. *R. sigma*, initially a member of the in-group, proved however to be a more suitable outgroup based on relationships demonstrated in the allozyme phenogram. When *R. epsilon* was used as an outgroup, a tree of markedly different topology was obtained, thereby confirming the findings of Barker *et al.* (1992).

The data obtained in this study confirm a close relationship between trees derived from electrophoretic and morphological data (Mickevich & Johnson, 1976). provided the same outgroup is utilised. The data presented resulted in trees which were simple enough to allow comparison with host trees by inspection rather than employing more sophisticated techniques, such as parsimony mapping (Brooks, 1988). There are few studies which compare tree topologies from morphological as opposed to electrophoretic data from parasites. Gardner (1991), in a study obtained of the aspidoderid nematode parasites of South American rodents, found that morphological and allozyme character sets differed by 10%, indicating a close similarity, while Barker (1991) found that morphological

Table III. Morphological characters used in phenetic and cladistic analyses of the *Rugopharynx delta* complex.

Taxa / Characters	*R. zeta*	*R. mawsonae*	*R. delta*	*R. omega*	*R. sigma*	*R. longibursaris*	*R. epsilon*
1. Buccal capsule trilobed	+	+	+	+	+	+	−
2. Dorsal lobe of bursa elongate	−	−	−	+	+	+	−
3. External branches of dorsal ray terminate in projections on surface of bursa	−	+	+	−	−	−	−
4. External branches of dorsal ray arise before bifurcation of internal branches	−	+	+	−	−	−	−
5. Ala of spicule tip enlarged	−	−	−	−	−	+	−
6. Spicule ala ends at tip abruptly	+	−	−	+	+	+	−
7. Spicule:body length ratio >1:5	−	−	+	+	+	+	−
8. Female tail:body length ratio >1:25	−	−	−	+	−	−	−
9. Gubernaculum present	+	−	−	−	+	−	−
10. Dorsal ray arcuate (−) or V-shaped	−	+	+	−	−	−	−
11. Deirid mid-oesophageal (−) or post-buccal (+)	−	+	+	−	+	−	−

Table IV. Input data matrix for allozyme data, with uniformative loci, *Acon*, *Ak*, *Hex*, *Idh*, *Pgam* and *Ugpp*, excluded.

R. zeta	1	1	0	1	0	1	0	1	2	1	1	−+	1	2	0	0
R. mawsonae	1	1	1	1	?*	0	2	1	1	0	1	−	1	1	1	1
R. delta	1	0	1	1	?	1	1	1	0	0	1	−	1	0	0	1
R. omega	1	1	1	1	2	1	1	1	1	2	0	1	0	4	1	0
R. sigma	0	0	1	0	1	0	1	0	1	2	−	0	1	2	−	0
R. longibursaris	1	1	1	1	2	1	1	1	1	2	1	1	0	3	1	0

*Result not interpreted into score.
+ No result available.

and allozyme data sets of boopid lice produced similar phylogenies, although the level of concordance was not quantified.

In the present study, the tree derived from allozyme data is based on a greater number of characters than are available from morphological examination. In addition, in dealing with a complex of very closely related nematode species, morphological differences are minor and the few morphological differences which do display between-species differences may not accurately reflect phylogenetic relationships.

In other electrophoretic studies of parasitic nematodes, comparisons of parasite trees have been made with that of the hosts. No definitive phylogenetic trees are available for the Macropodidae, based on either morphological (Flannery, 1989), electrophoretic (Richardson & McDermid, 1978; Baverstock *et al.*, 1985) or immunological data (Kirsch, 1977; Baverstock *et al.*, 1989). With respect to the present study, however, there is little doubt from the studies cited that the species of the subgenus *Notamacropus* are closely related (*M. dorsalis*, *M. parma*, *M. parryi*, *M. rufogriseus*) and the genera *Petrogale* and *Thylogale* are also closely related, with *Thylogale* demonstrating ancestral character states.

The electrophoretic analysis of the members of the *R. delta* complex is consistent with an hypothesis of parallel evolution between host and parasite. *R. sigma*, with the greatest number of ancestral characters states, occurs in the host genus with ancestral character states, and the remaining species, with derived character states occur in host with derived character

Table V. Input data matrix for morphological data, based on character scorings in Table III.

R. zeta	1	0	0	0	0	1	0	0	1	0	0
R. mawsonae	1	0	1	1	0	0	0	0	0	1	1
R. delta	1	0	1	1	0	0	1	1	0	1	1
R. longibursaris	1	1	0	0	1	1	1	0	0	0	0
R. omega	1	1	0	0	0	1	1	0	0	0	0
R. sigma	1	1	0	0	0	1	1	0	1	0	1
R. epsilon	0	0	0	0	0	0	0	0	0	0	0

states. In the case of *R. zeta* in *Petrogale* spp., the relationship is presumably close enough to allow host switching into *Thylogale thetis*. Host switching also occurs in the case of *R. mawsonae* and *R. omega*, but it is invariable to closely related host species, and usually in situations where the two host species are sympatric. *Macropus* (*Notamacropus*) is a more recent group in the fossil record than *Thylogale* (see Archer, 1984) and a diversification of nematode taxa has presumably occurred in wallabies of this subgenus. This hypothesis for the evolution of the *R. delta* complex is consistent with the notion that the Cloacininae Stossich, 1899 diversified first of all in *Thylogale* spp. and subsequently in *Macropus* (see Beveridge, 1986). It also parallels the evolution of the trichostrongyloid genera *Austrostrongylus* Chandler, 1924 and *Sutarostrongylus* Beveridge & Durette-Desset, 1986 first in *Thylogale* and *Petrogale*, then in *Macropus* (Beveridge & Durette-Desset, 1986).

In the case of the *R. longibursaris* – *R. omega* species pair, Chilton *et al.* (1993) have advanced a proposal for the evolution of the species allopatrically during the separation of Tasmania from mainland Australia, with the probable re-invasion of western Victoria by *R. longibursaris* with its host. The two nematode species are currently allopatric in their distribution in Victoria (Chilton *et al.*, 1993), but the above analyses are consistent with the hypothesis of Chilton *et al.* (1993). *R. omega* "switches" to the related host *M. parryi* but only where *M. parryi* is sympatric with *M. rufogriseus* (see Beveridge, 1982; unpublished observations).

R. delta and *R. mawsonae* by contrast occur in the same host species *M. dorsalis*, and usually occur in mixed infections. Possible explanations for this association included sympatric speciation or the evolution of one of the nematodes in a now extinct host species from which it "switched" prior to the extinction of that host (Page, 1991). However, *R. mawsonae* is also parasitic in *M. parma*. It may have evolved in *M. parma* and because of the very close phylogenetic relationship between *M. dorsalis* and *M. parma* (see Baverstock *et al.*, 1985; Flannery, 1989), including their ability to interbreed (Close & Lowry, 1990), switched to *M. dorsalis*. Currently *M. parma* and *M. dorsalis* are broadly sympatric in part of the geographical range of *M. dorsalis* (see Maynes, 1983; Kirkpatrick, 1983). All of the material of *R. mawsonae* in *M. dorsalis* has been collected outside the geographical range of *M. parma* (see Beveridge *et al.*, 1994). The current data do not support the hypothesis (Beveridge *et al.*, 1989), based on ecological data, that *R. zeta* in *Petrogale* spp. was derived through a host switch from *M. dorsalis*.

In summary, the electrophoretic analysis of members of the *R. delta* complex has not provided a definitive phylogeny, but has provided additional hypotheses on the evolution of these nematodes which were not evident from morphological comparisons. The electrophoretic data are consistent with broad co-evolution between hosts and parasites, a result which concords with other studies of nematodes in macropodid marsupials. Further studies, using additional techniques and including nematodes whose current status is uncertain such as those resembling *R. omega* parasitic in *Thylogale thetis*, are needed to confirm or reject the hypotheses presented here based on electrophoretic analyses.

Acknowledgements

Our thanks are due to Dr R. Gasser for assistance with computer analyses to Dr S.C. Barker and Mr M. Adams for advice and to Dr D.M. Spratt yet again for his forbearance in commenting on drafts of the manuscript. The work was supported financially by the Australian Research Council.

References

Archer, M. (1984) The Australian marsupial radiation. *In:* Archer, M. & Clayton, G. (Eds). *Vertebrate zoogeography and evolution in Australasia*. Western Australia: Hesperian Press, pp. 633–808.

Barker, S.C. (1991) Phylogeny of the *Heterodoxus octoseriatus* group (Phthiraptera: Boopidae) from rock-wallabies (Marsupialia: *Petrogale*). *Systematic Parasitology*, **19**, 17–24.

Barker, S.C., Briscoe, D.A. & Close, R.L. (1992) Phylogeny inferred from allozymes in the *Heterodoxus octoseriatus* group of species (Phthiraptera: Boopidae). *Australian Journal of Zoology*, **40**, 411–422.

Baverstock, P.R., Adams, M. & Beveridge, I. (1985) Biochemical differentiation of bile duct cestodes and their marsupial hosts. *Molecular Biology and Evolution*, **2**, 321–337.

Baverstock, P.R., Richardson, B.J., Birrell, J. & Krieg, M. (1989) Albumin immunologic relationships of the Macropodidae (Marsupiealia). *Systematic Zoology*, **38**, 38–50.

Beveridge, I. (1982) A taxonomic revision of the Pharyngostrongylinea Popova (Nematoda: Strongyloidea) from macropod marsupials. *Australian Journal of Zoology, Supplementary Series*, no. **83**, 1–150.

Beveridge, I. (1986) Coevolutionary relationships of the helminth parasites of Australian marsupials. *In*: Stone, A.R. & Hawksworth, D.L. (Eds). *Coevolution and systematics*. Oxford: Clarendon Press, pp. 93–117.

Beveridge, I., Spratt, D.M., Close, R.L., Barker, S.C. & Sharman, G.B. (1989) Helminth parasites of rock-wallabies, *Petrogale* spp. (Marsupialia) from Queensland. *Australian Wildlife Research*, **39**, 691–702.

Beveridge, I., Chilton, N. & Andrews, R.H. (1993) Sibling species within *Macropostrongyloides baylisi* (Nematoda: Strongyloidea) from macropodid marsupials. *International Journal for Parasitology*, **23**, 21–33.

Beveridge, I., Chilton, N. & Andrews, R.H. (1994) A morphological and electrophoretic study of *Rugopharynx zeta* (Johnston & Mawson, 1939) (Nematoda: Strongyloidea) with the description of a new species, *R. mawsonae*, from the black-striped wallaby, *Macropus dorsalis* (Marsupialia: Macropodidae). *Systematic Parasitology*, **27**, 159–171.

Beveridge, I. & Durette-Desset, M.-C. (1986) New species of *Austrostrongylus* Chandler, 1924 (Nematoda, Trichostrongyloidea), from Australian marsupials with a redescription of *A. minutus* Johnston & Mawson, 1938, and description of a new genus, *Sutarostrongylus*. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, 4ème série, **8**, 145–170.

Brooks, D.R. (1988) Macroevolutionary comparisons of host and parasite phylogenies. *Annual Review of Ecology and Systematics*, **19**, 235–259.

Chilton, N.B., Beveridge, I. & Andrews, R.H. (1992) Detection by allozyme electrophoresis of cryptic species in *Hypodontus macropi* (Nematoda: Strongyloidea) from macropodid marsupials. *International Journal for Parasitology*, **22**, 271–280.

Chilton, N.B., Beveridge, I. & Andrews, R.H. (1993) Electrophoretic comparison of *Rugopharynx longibursaris* Kung and *Rugopharynx omega* Beveridge (Nematoda: Strongyloidea), with the description of *R. sigma* n.sp. from pademelons, *Thylogale* spp. (Marsupialia: Macropodidae). *Systematic Parasitology*, **26**, 159–169.

Close, R.L. & Lowry, P.S. (1990) Hybrids in marsupial research. *Australian Journal of Zoology*, **37**, 259–267.

Eldridge, M.D.B. & Close, R.L. (1992) Taxonomy of rock wallabies, *Petrogale* (Marsupialia: Macropodidae). I. A revision of the eastern *Petrogale* with the description of three new species. *Australian Journal of Zoology*, **40**, 605–625.

Flannery, T.F. (1989) Phylogeny of the Macropodoidea: a study in convergence. *In*: Grigg, G., Jarman, P. & Hume, I. (Eds). *Kangaroos, wallabies and rat-kangaroos*. New South Wales: Surrey Beatty, pp. 1–46.

Gardner, S.L. (1991) Phyletic coevolution between subterranean rodents of the genus *Ctenomys* (Rodentia: Hystricognathi) and nematodes of the genus *Paraspidodera* (Heterakoidea: Aspidoderidae) in the Neotropics: temporal and evolutionary implications. *Zoological Journal of the Linnean Society*, **102**, 169–201.

Georges, A. & Adams, M. (1992) A phylogeny for Australian chelid turtles based on allozyme electrophoresis. *Australian Journal of Zoology*, **40**, 453–476.

Kirkpatrick, T.H. (1983) Black-striped wallaby, *Macropus dorsalis*. *In*: Strahan, R. (Ed). *The Australian Museum complete book of Australian mammals*. Sydney: Angus & Robertson, p. 238.

Kirsch, J.A.W. (1977) The comparative serology of Marsupialia and a classification of marsupials. *Australian Journal of Zoology, Supplementary Series*, no. **52**, 1–152.

Maynes, G. (1983) Parma wallaby, *Macropus parma*. *In*: Strahan, R. (Ed.). *The Australian Museum complete book of Australian mammals*. Sydney: Angus & Robertson, pp. 230–231.

Mickevich, M.F. & Johnson, M.S. (1976) Congruence between morphological and allozyme data in evolutionary inference and character evolution. *Systematic Zoology*, **25**, 260–270.

Page, R.D.M. (1991) Clocks, clades and cospeciation: comparing rates of evolution and timing of co-speciation events in host-parasite assemblages. *Systematic Zoology*, **40**, 188–198.

Richardson, B.J. & McDermid, E.M. (1978) A comparison of genetic relationships within the Macropodidae as determined from allozyme, cytological and immunological data. *Australian Mammalogy*, **2**, 43–51.

Sneath, P.H.A. & Sokal, R.R. (1973) *Numerical taxonomy: the principles and practice of numerical classification*. San Francisco: W.H. Freeman & Co., 573 pp.

Swofford, D.L. (1991) *PAUP: Phylogenetic analysis using parsimony* (Version 3.OS). Illinois: Illinois Natural History Museum.

Wiley, E.O. (1981) *Phylogenetic systematics. The theory and practice of phylogenetic systematics*. New York: John Wiley, 439 pp.