Aust. J. Zool., 1992, **40**, 411–22

Phylogeny Inferred from Allozymes in the *Heterodoxus octoseriatus* Group of Species (Phthiraptera : Boopiidae)

S. C. Barker[A], *D. A. Briscoe*[B] *and R. L. Close*[C]

[A] Department of Parasitology, University of Queensland, Qld 4072, Australia.
[B] School of Biological Sciences, Macquarie University, N.S.W. 2109, Australia.
[C] School of Business and Technology, University of Western Sydney, Campbelltown, N.S.W. 2560, Australia.

Abstract

Phenetic and phylogenetic relationships in the *Heterodoxus octoseriatus* group of species were explored with data from 21 putative allozyme loci. The phenetic analyses and some of the cladistic analyses (maximum parsimony) were consistent with a phenetic analysis of morphological characters in that they indicated two main lines of evolution in the *H. octoseriatus* group. These culminated in two groups of species: (i) *H. harrisoni*, *H. hughendensis*, *H. closei*, *H. maynesi*, *H. octoseriatus*, *H. lesouefi*, *H. briscoei* and *H. insulatus*, and (ii) *H. murrayi*, *H. insularis* and *H. orarius*. The allozyme and morphological analyses, however, differed in the arrangement of species within the two main groups. Other cladistic analyses revealed the first group of lice, but not the second group. A hypothesis proposed for the evolution of the *H. octoseriatus* group involves widespread host-switching followed by the expansion of the geographic ranges of some lice at the expense of others. The evolution of host–parasite associations among rock-wallabies and lice from the *H. octoseriatus* group demonstrates how tangled the history of host–parasite associations may become.

Introduction

Rock-wallabies (*Petrogale* spp.) are infested by lice from two groups of species: the *Heterodoxus ampullatus* group and the *H. octoseriatus* group (Clay 1981; Barker 1991*a*). The 11 species in the *H. octoseriatus* group are restricted to rock-wallabies in eastern Australia (Barker and Close 1990; see also fig. 3 in Barker 1991*c*).

This paper is one of a series on the systematics (Barker 1991*a*, 1991*b*), host associations and zoogeography (Barker and Close 1990), evolution of host associations (Barker 1991*c*) and genetics (Barker *et al.* 1991*a*, 1991*b*) of the *H. octoseriatus* group. Phylogenetic relationships among the rock-wallabies infested by species of the *H. octoseriatus* group have also been studied (Eldridge *et al.* 1988, 1989, 1990, 1991; Sharman *et al.* 1990).

In the present study phylogeny in the *H. octoseriatus* group is inferred from cladistic analyses of allozymes to provide an independent test of a phylogeny inferred from a phenetic analysis of morphological characters (Barker 1991*b*). This may lead to a more robust phylogeny that will in turn strengthen tests of the host–parasite coevolution model (see Barker 1991*c*) for the *H. octoseriatus* group and their hosts.

Materials and Methods

On the basis of allozyme electrophoresis (cellulose acetate) considerable genetic variation was found in four of the 11 species in the *H. octoseriatus* group: *H. insularis*, *H. orarius*, *H. octoseriatus* and *H. maynesi* (Barker *et al.* 1991*b*). The variation was considered insufficient, however, to reject the null hypothesis that the species recognised on morphological criteria were 'good' biological species (Barker *et al.* 1991*b*). Nonetheless, in the present study, we attempted to account for this variation by analysing the data in two different ways: data set 1 held the recognised species (11 taxa plus the outgroup), whereas data set 2 held the recognised species but each of the four variable species was divided into two taxa (15 taxa plus the outgroup, Table 1).

0004-959X/92/040411$05.00

In all, 721 lice were collected from 49 hosts at 38 localities (colonies) in Queensland, Australia (table 1 in Barker *et al.* 1991*b*). Lice were identified to species, and enzymes were extracted and subjected to electrophoresis (see Barker *et al.* 1991*b*). A total of 35 putative loci was screened but mobilities from only 21 could be reliably scored in all species in the *H. octoseriatus* group and the outgroup (Barker *et al.* 1991*b*). The outgroup was *Heterodoxus* sp. 14, a member of the *H. ampullatus* group from the Proserpine rock-wallaby, *Petrogale persephone* (host number S769, Gloucester I., Queensland).

Data Transformation and Analysis

In this study most of the genetic variation among taxonomic units occurred as fixed gene differences. Data of this form are most suited to analysis based on the proportion of fixed gene differences. Other genetic distance measures, such as Nei's D (Nei 1972) and Rogers' R (Rogers 1972), were designed primarily for population studies, where a significant proportion of alleles are shared among populations. The proportion of fixed gene differences was analysed phenetically by the unweighted pair group method with arithmetic means (average linkage) (Sneath and Sokal 1973) and cladistically (maximum parsimony) by the branch-and-bound option in PAUP version 3.0S; the latter is guaranteed to find the shortest tree (Swofford 1991). Cladistic trees were rooted in two ways. Initially, we used *H.* sp. 14 as the outgroup (above). The topology of trees from the phenetic and cladistic analyses of data set 2, however, differed markedly. This led us to test the utility of the outgroup by excluding it and rooting the tree in the middle of the longest branch (midpoint root option in PAUP). Equally parsimonious trees are presented here as 50% majority-rule consensus trees (Swofford 1991).

In the cladistic analysis, putative loci were used as characters and the putative alleles used as character states. There were few cases where a species had more than one allele at a locus. Indeed, except for *H. octoseriatus*, two alleles occurred at individual loci in six species: *H. harrisoni* (AK-A), *H. insulatus* (ADA-A, EST), *H. insularis* (MDH-A, IDH-C), *H. orarius* (ADA-C, ADA-A, IDH-C, PK, AK-A), *H. murrayi* (ADA-A) and *H. maynesi* (PK, ME). For the cladistic analyses, where there was more than one allele at a locus we ignored the allele that occurred at the fewest sites and/or in the fewest individual lice (Table 1; raw data in table 1 in Barker *et al.* 1991*b*). In addition, we excluded *H. octoseriatus* from the cladistic analyses because at 11 of the 17 loci scored this species showed more than one allele (Table 1) and for several loci it was unclear which allele should be ignored [*H. octoseriatus* contains extraordinary intraspecific genetic variation associated with a hybrid zone between two taxa of hosts (Barker *et al.* 1991*a*, 1991*b*)].

In summary, there were two sets of data. Data set 1 contained the 11 species in the *H. octoseriatus* group plus the outgroup species; one of these, *H. octoseriatus*, was excluded from the cladistic analysis (but not from the phenetic analysis). Data set 2 contained these 12 species plus four additional operational taxonomic units (OTUs) derived from *H. insularis*, *H. orarius*, *H. octoseriatus* and *H. maynesi*; the two OTUs derived from *H. octoseriatus* were excluded from the cladistic analysis (but not from the phenetic analysis). In phenetic analyses an outgroup is not required to root the trees (trees are rooted by the method); thus, *H.* sp. 14 was excluded from both phenetic analyses.

In cladistic analyses of putative alleles inferred from electromorphs it is debatable whether alleles should be treated as unordered character states, ordered character states or otherwise (e.g. Buth 1984). Where character states are unordered each may transform to any other state with equal cost. Thus, it is assumed that it is equally likely that any character state will transform to any other character state. Where character states are ordered according to their relative mobility it is assumed that differences in mobility have accumulated in a stepwise fashion, for example, for three electromorphs (A, B, C) with increasing mobility (cathode to anode) B may transform to either A or C with equal cost, but A must transform to B before it transforms to C, and vice versa. It might be argued that alleles should be treated as unordered character states because this requires no *a priori* assumptions about the evolution of electromorphs. In fact, *a priori* assumptions are made whether the putative alleles are treated as ordered or unordered character states (see above). The topology of cladograms from alleles analysed as unordered and ordered character states may differ substantially (see below). In this study the data were analysed both ways.

Results

Most genetic variation among the 11 species occurred as fixed gene differences (Table 1). The outgroup, *H.* sp. 14, had 60–100% fixed gene differences (mean 82·2%) with respect to the 11 species in the *H. octoseriatus* group (Table 2) and 61·5–100% fixed gene

Table 1. Matrix of alleles detected in the species and operational taxonomic units (OTUs) of the *Heterodoxus octoseriatus* group and *Heterodoxus* sp. 14 (the outgroup)

Multiple loci are distinguished numerically according to increasing electrophoretic mobility. Alleles were designated alphabetically in order of increasing electrophoretic mobility. In the cladistic analyses alleles from *H. octoseriatus* were ignored

OTU	Enzymes																				
	ACP-C	ADA-C	ADA-A	MDH-C	MDH-A	IDH-C	IDH-A	GOT-C	GOT-A	ALDOL	αGPD	ENOL-A	FUM	EST	GDA-C	PK	ME	PEP	G6PD	AK-A	AK-C
H. harrisoni	b	b	b	b	a	b	c	a	b	b	b	b	a	b	b	b	b	a	b	c/d[A]	b
H. hughendensis	–	b	b	b	a	–	–	–	–	–	–	–	–	–	–	b	a	–	–	–	–
H. closei	b	b	b	b	a	b	–	–	–	–	–	–	–	b	–	b	–	–	–	–	–
H. lesouefi	–	b	b	b	a	b	c	a	–	–	b	b	a	a	–	a	c	a	b	e	–
H. briscoei	–	b	b	b	a	b	–	–	–	–	b	–	a	b	–	c	a	–	b	–	–
H. insulatus	b	b	b/e[A]	b	a	b	a	a	a	b	b	b	a	a[A]/b	b	b	a	a	a	d	b
H. insularis	b	c	a	a	b	b	c	a	b	b	a	–	a	b	b	a	c	–	b	c	–
H. insularis-Glen Harding	–	c	–	a	a[B]	d[B]	–	a	–	–	a	b	–	b	–	a	–	d	–	c	–
H. orarius	b	c	b[A]/c	a	a	a[A]/b	c	a	–	b	a	b	a	b	b	a	a	d	–	a[A]/d	a
H. orarius-Laura	–	e[B]	c	a	–	b	–	–	b	b	–	–	–	b	b	b[B]	a	–	–	–	–
H. murrayi	–	c	b/c[A]	b	a	b	–	a	b	b	a	b	a	b	b	b	a	d	–	c	–
H. octoseriatus-Northern	–	b	a/b	b/d	a/b/c	b	a	–	b	b	c	b/c	a	a	b	a/b	a/b	–	a/b	–	b
H. octoseriatus-Southern	–	b	d	b	c	b	a/b	–	b/c	a	b	b	a	–	–	b	b	–	b	–	–
H. maynesi	–	b	b	b	a	b	–	–	–	–	b	b	a	a	–	b[B]	b	–	–	–	–
H. maynesi-Whitsunday I.	b	b	b	b	a	b	a	a	b	b	b	b	a	a	b	a	a[B]	b	a	c	a
H. sp. 14	a	d	–	c	b	c	b	a	c	a	d	a	a	–	a	d	d	d	b	b	a

[A] Alleles ignored in data sets 1 and 2. [B] Alleles ignored in data set 1 only.

Table 2. Matrix of fixed gene differences among the 11 species of the *Heterodoxus octoseriatus* group and the outgroup, *Heterodoxus* sp. 14

The lower matrix contains the percentage of fixed gene differences, and the upper matrix contains the number of loci used in the comparison

	Heterodoxus											
	harrisoni	*closei*	*lesouefi*	*briscoei*	*insulatus*	*insularis*	*orarius*	*murrayi*	*maynesi*	*octoseriatus*	*hughendensis*	sp. 14
Heterodoxus												
harrisoni	–	8	16	11	21	20	20	17	21	17	6	19
closei	0·0	–	7	7	8	8	8	7	8	7	5	6
lesouefi	25·0	28·6	–	11	16	16	15	14	16	13	6	14
briscoei	18·2	14·3	27·3	–	11	11	10	10	11	11	6	9
insulatus	19·0	0·0	31·3	18·2	–	20	20	17	21	17	6	19
insularis	35·0	50·0	43·8	54·5	55·0	–	19	17	20	16	6	18
orarius	30·0	25·0	46·7	40·0	35·0	15·8	–	17	20	16	6	18
murrayi	23·5	14·3	50·0	30·0	29·4	23·5	11·8	–	17	14	6	15
maynesi	23·8	12·5	31·3	27·3	19·0	45·0	35·0	23·5	–	17	6	19
octoseriatus	11·8	14·3	23·1	18·2	5·9	43·8	37·5	21·4	5·9	–	6	15
hughendensis	16·7	0·0	33·3	16·7	0·0	83·3	33·3	16·7	0·0	0·0	–	5
sp. 14	84·2	100·0	78·6	77·8	89·5	72·3	77·8	80·0	84·0	60·0	100·0	–

differences (mean 83·4%) with respect to the 15 OTUs of the *H. octoseriatus* group (table 5 in Barker *et al.* 1991*b*).

Cladograms from unordered character states were shorter (as expected on theoretical grounds) and had higher consistency indices than those from ordered character states (Table 3).

Table 3. Number of equally short trees, number of steps and consistency indices (excluding uninformative characters) from cladistic analyses of data sets 1 and 2

OTUs, operational taxonomic units

	Character states	Number of equally short trees	Number of steps	Consistency Index
Trees rooted with the outgroup				
Data set 1 (11 species)	Ordered	162	48	0·674
	Unordered	375	38	0·793
Data set 2 (14 OTUs)	Ordered	781	52	0·667
	Unordered	1827	40	0·812
Trees rooted in middle of the longest branch (outgroup excluded)				
Data set 1 (10 species)	Ordered	841	31	0·655
	Unordered	375	25	0·714
Data set 2 (13 OTUs)	Ordered	1800	35	0·677
	Unordered	1827	27	0·750

Data Set 1 (10–11 Species)

The phenetic analysis (Fig. 1), the cladistic analyses rooted with the outgroup and based on ordered states (Fig. 2), the cladistic analyses rooted at the midpoint of the longest branch and based on unordered (Fig. 3) and on ordered character states (not shown because the topology was identical to that of Fig. 3) revealed two main clusters of taxa within the *H. octoseriatus* group: (i) *H. murrayi*, *H. insularis* and *H. orarius*, and (ii) the remaining species. The cladistic analysis rooted with the outgroup and based on unordered characters showed the latter cluster as monophyletic, but did not support monophyly for *H. murrayi*, *H. insularis* and *H. orarius* (Fig. 4); i.e. only (ii) from above was present. The arrangement of taxa within clusters in the cladistic and the phenetic analyses differed (Figs 1–4).

Data Set 2 (14–15 OTUs)

The phenetic analysis of the 15 OTUs revealed two main clusters: the OTUs derived from *H. murrayi*, *H. orarius* and *H. insularis*, and the 10 remaining OTUs (Fig. 5). In the cladistic analysis rooted with the outgroup and based on ordered character states there were four clusters in the *H. octoseriatus* group: (i) *H. insularis*, (ii) *H. murrayi*, (iii) *H. orarius*, *H. orarius*-Laura and *H. insularis*-Glenharding, and (iv) the eight remaining OTUs (Fig. 6). In the cladistic analysis rooted with the outgroup and based on unordered character states the latter eight OTUs clustered together, but the other OTUs were arranged otherwise (Fig. 7). In the cladistic analyses rooted at the midpoint of the longest branch and based on unordered (Fig. 8) and on ordered character states (not shown because the topology was similar to that of Fig. 7, see caption to Fig. 8), there were two clusters of species: the OTUs derived from *H. murrayi*, *H. orarius* and *H. insularis*, and the eight remaining OTUs (Fig. 8).

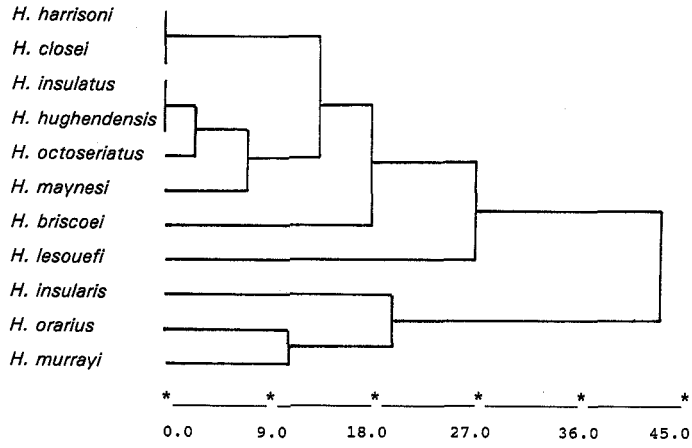

Fig. 1. Unweighted average cluster (phenetic analysis) of fixed gene differences among 11 species in the *Heterodoxus octoseriatus* group. Scale is percentage of fixed gene differences.

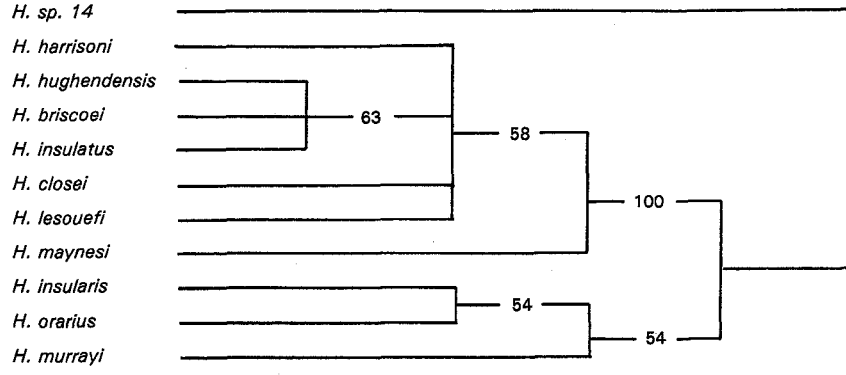

Fig. 2. Consensus cladogram for 10 species in the *Heterodoxus octoseriatus* group and the outgroup *Heterodoxus* sp. 14. The cladogram was rooted with the outgroup, character states were ordered; the consistency index (uninformative characters excluded) is 0·674, and the number of steps is 48. Numbers on branches indicate the percentage of trees containing the branch shown.

Discussion

Phylogenies and Character Evolution

In all the trees (eight consensus cladistic and two phenetic trees) *H. harrisoni*, *H. hughendensis*, *H. closei*, *H. maynesi*, *H. lesouefi*, *H. briscoei*, *H. insulatus* (=group A) and, when included, *H. octoseriatus* clustered together (*H. octoseriatus* was excluded from the cladistic analyses). In four trees *H. murrayi*, *H. insularis* and *H. orarius* (=group B) clustered together; in another three the OTUs derived from these species clustered together; and in another the two OTUs derived from *H. orarius* and one of the OTUs from *H. insularis* clustered together. The arrangement of taxa within the two main groups, however, differed markedly among cladograms. Thus, the only conclusions that can be drawn from these analyses are that there have apparently been at least two main lines

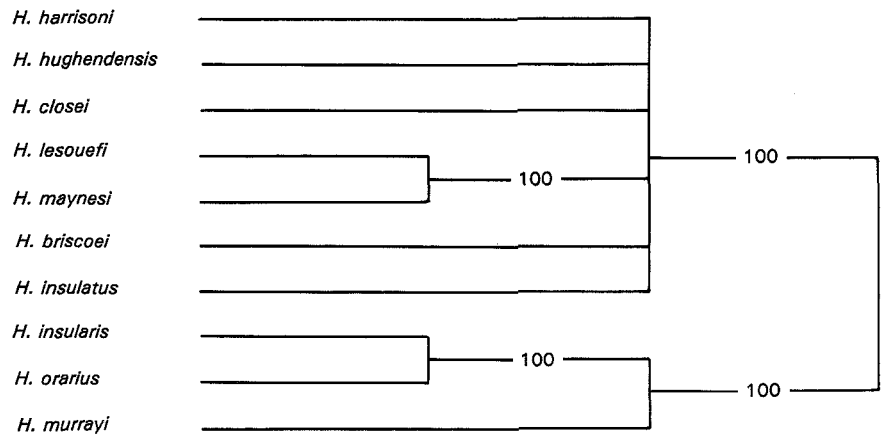

Fig. 3. Consensus cladogram for 10 species in the *Heterodoxus octoseriatus* group. The cladogram was rooted at the midpoint of the longest branch, character states were unordered (the cladogram based on ordered character states had topology identical to that shown); the consistency index (uninformative characters excluded) is 0·714 and the number of steps is 25. Numbers on branches indicate the percentage of trees containing the branch shown.

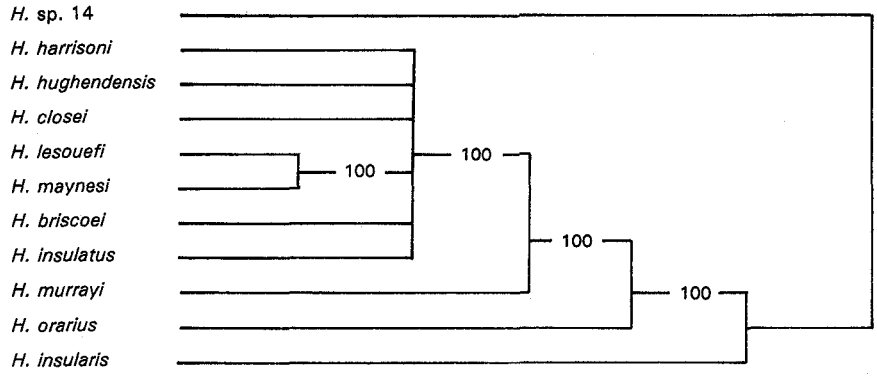

Fig. 4. Consensus cladogram for 10 species in the *Heterodoxus octoseriatus* group and the outgroup *Heterodoxus* sp. 14. The cladogram was rooted with the outgroup, character states were unordered; the consistency index (uninformative characters excluded) is 0·793 and the number of steps is 38. Numbers on branches indicate the percentage of trees with the branch shown.

of evolution in the *H. octoseriatus* group. One line of evolution led to group A and *H. octoseriatus*. A second line of evolution led to group B, but this conclusion is less well supported than the first.

The trees inferred from allozymes are consistent with a phylogeny inferred from a phenetic analysis of morphological characters (Barker 1991*b*) in that the species in group A, together with *H. octoseriatus* and their composite OTUs, formed a cluster, to the exclusion of the species in group B (and their composite OTUs). The phylogenies inferred from morphology and allozymes, however, differed in their arrangement of taxa within both groups. Further, group B, which was present in the tree based on morphology, was not present in all of the trees derived from allozymes.

A number of factors may have contributed to the inconsistency among the trees from phenetic and cladistic analyses. First, data were not collected for some species at some loci

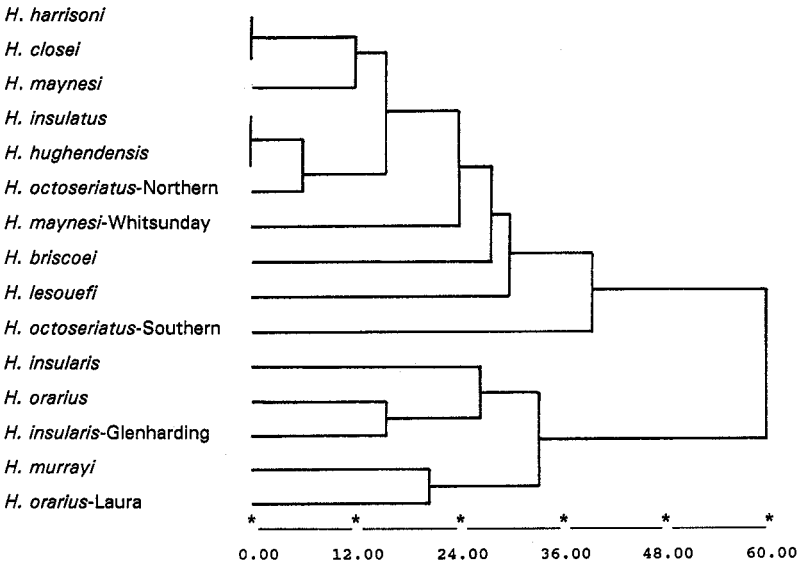

Fig. 5. Unweighted averaged cluster (phenetic analysis) of fixed gene differences among 15 operational taxonomic units (OTUs) in the *Heterodoxus octoseriatus* group. Scale is percentage of fixed gene differences.

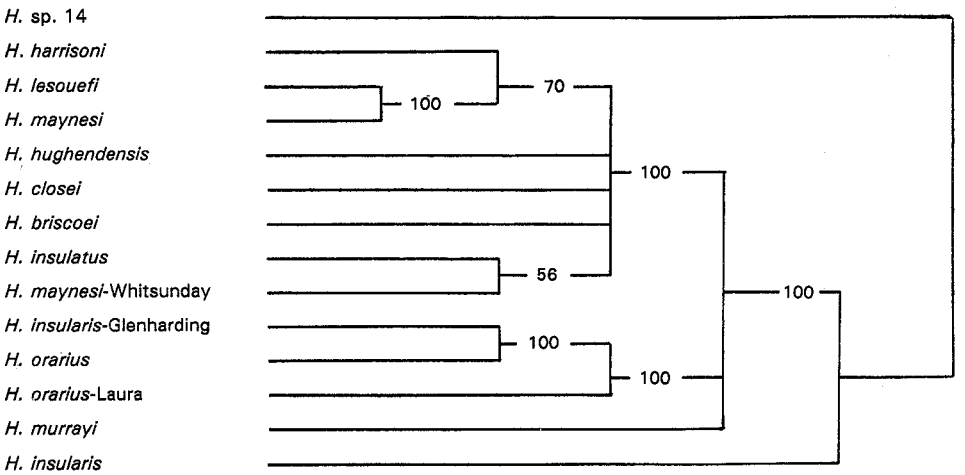

Fig. 6. Consensus cladogram for 13 operational taxonomic units (OTUs) in the *Heterodoxus octoseriatus* group and the outgroup *Heterodoxus* sp. 14. The cladogram was rooted with the outgroup, character states were ordered; the consistency index (uninformative characters excluded) is 0·667 and the number of steps is 52. Numbers on branches indicate the percentage of trees with the branch shown.

because insufficient lice were available. This reflects the problems associated with collecting lice from rock-wallabies. Rock-wallabies generally occurred in remote regions, were difficult to catch and were lightly infested (the median infestation of 92 rock-wallabies was 12 adult lice; Barker 1988). As few as 11 lice per species were available for genetic study (*H. closei*; table 1 in Barker *et al.* 1991*b*).

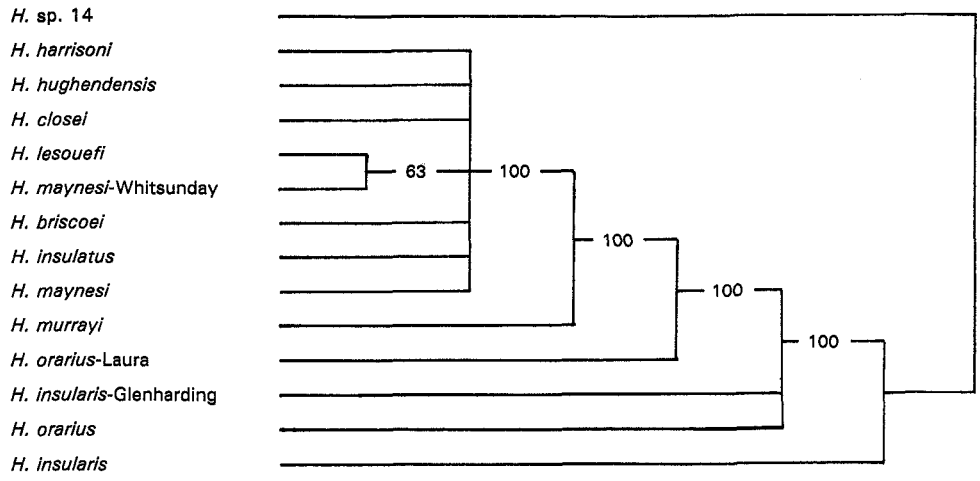

Fig. 7. Consensus cladogram for 13 operational taxonomic units (OTUs) in the *Heterodoxus octoseriatus* group and the outgroup *Heterodoxus* sp. 14. The cladogram was rooted with the outgroup, character states were unordered; the consistency index (uninformative characters excluded) is 0·812 and the number of steps is 40. Numbers on branches indicate the percentage of trees with the branch shown.

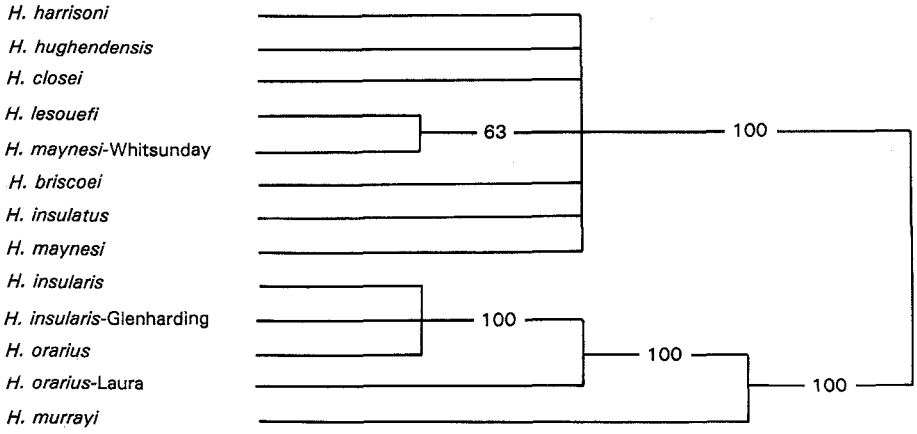

Fig. 8. Consensus cladogram for 13 operational taxonomic units (OTUs) in the *Heterodoxus octoseriatus* group. The cladogram was rooted at the midpoint of the longest branch, character states were unordered (the cladogram based on ordered character states had the two main clusters present in the cladogram shown, but the arrangement of species within these clusters differed from that of the cladogram shown); the consistency index (uninformative characters excluded) is 0·750 and the number of steps is 27. Numbers on branches indicate the percentage of trees containing the branch shown.

Second, the outgroup, *H.* sp. 14, may have been too distant from the *H. octoseriatus* group. This idea was tested by excluding *H.* sp. 14 and analysing the data with the midpoint root option in PAUP (above). Thus, an outgroup was not used and the root was placed in the middle of the longest branch. Trees from these analyses revealed two clusters of species: group A plus *H. octoseriatus*, and group B. Moreover, the degree of resolution at the base of trees generally increased in both sets of analyses (Figs 3, 8). Thus, *H.* sp. 14 was probably too distant from the ingroup and this led to a loss of resolution at the first

dichotomy within the *H. octoseriatus* group. Species from the *Heterodoxus calabyi* group, which is the sister-group of the *H. octoseriatus* group (Barker 1991*b*), may have been better suited, but were not available.

Third, rates of evolution of electromorphs may have been widely different in the *H. octoseriatus* group – differential rates of evolution may, in particular, confound phenetic analyses (Richardson *et al.* 1986). Fourth, widespread inbreeding (Barker *et al.* 1991*b*) may have contributed to variability ('noise') in the data if phylogenetically informative alleles were eliminated by chance. Finally, additional variability may have been added to the data through the generation of novel alleles at zones of parapatry between different taxa of lice (see Barker and Close 1990), and through introgression of alleles from one species into another.

The trees based on biochemical characters have allowed a problem raised by the analysis of morphological characters to be addressed. The presence of a sclerotised ridge on the dorsal plate of the male genitalia of *H. insulatus* indicated that this species might be more closely related to *H. murrayi*, *H. insularis* and *H. orarius* than to the remaining seven species in the *H. octoseriatus* group (Barker 1991*b*). In the present study *H. insulatus* formed a cluster with the latter group in all the trees inferred from allozymes. Thus, as suggested by Barker (1991*b*), the similarity of this ridge to the stout sclerotised point seen in *H. murrayi*, *H. insularis* and *H. orarius* appears to be homoplastic.

Evolution of the H. octoseriatus *Group*

Phenetic and cladistic analyses of allozymes (this study), and the morphological analyses (Barker 1991*b*), indicate two main lines of evolution in the *H. octoseriatus* group. There may have been two main lines of evolution in their *Petrogale* hosts also. The favoured phylogeny of Eldridge *et al.* (1991, fig. 4) comprised two main groups of rock-wallabies: *P. inornata*, *P. assimilis assimilis* and *P. godmani* on the one hand, and the Cape York species, *P. penicillata penicillata*, *P. penicillata herberti*, *P. assimilis*-Mt Claro and *P. assimilis*-Mareeba on the other. One explanation for the evolution of associations between these rock-wallabies and species in the *H. octoseriatus* group is that the primary splits in the louse and host trees occurred at a similar time and the split in the host tree led to the split in the louse tree. In the first branch, three rock-wallaby taxa (*P. inornata*, *P. a. assimilis* and *P. godmani*) evolved from the original host, and three species of lice (*H. murrayi*, *H. insularis* and *H. orarius*) evolved from its louse. A second branch of evolution culminated in five rock-wallaby taxa (the Cape York species, *P. p. penicillata*, *P. p. herberti*, *P. assimilis*-Mt Claro and *P. assimilis*-Mareeba) and eight species of lice (*H. harrisoni*, *H. hughendensis*, *H. closei*, *H. maynesi*, *H. octoseriatus*, *H. lesouefi*, *H. briscoei* and *H. insulatus*).

To account for present host–parasite associations the following host-switching and range expansion would also have occurred (see also fig. 3 in Barker 1991*c* and figs 1–5 in Barker and Close 1990). In each case the colonising louse apparently excluded the original louse (individual rock-wallabies infested with more than one species of louse have not been found: Barker 1988). *H. murrayi* colonised the Cape York species and *P. assimilis*-Mareeba; *H. orarius* colonised the Cape York species; *H. insularis* colonised *P. assimilis*-Mt Claro and *P. assimilis*-Mareeba; the ancestor of *H. harrisoni*, *H. hughendensis* and *H. closei*, together with *H. insulatus* and *H. lesouefi*, colonised various populations of *P. a. assimilis*; and *H. maynesi* and *H. octoseriatus* colonised *P. inornata*.

This sequence of events, as complicated as it is, is probably oversimplified. For example, the presence of *H. insularis* on *P. inornata* at its zone of parapatry with *P. a. assimilis* (fig. 3 in Barker and Close 1990) is consistent with the above argument but this association probably arose by reversion to the archetypal association through recolonisation (see Barker and Close 1990 for evidence of host-switching at this zone of parapatry).

The evolution of associations among species of lice of the *H. octoseriatus* group and taxa of *Petrogale* demonstrates how tangled the history of host–parasite associations may be.

Moreover, this has apparently occurred in a group of parasites that are highly dependent on, and that might be expected to coevolve closely with, their hosts (Barker 1991*c*).

Acknowledgments

We thank M. D. Murray, A. Gooley, T. H. Cribb, R. W. Murphy and two anonymous referees for criticising earlier drafts, D. Scott for drawing the figures, D. L. Swofford for providing PAUP 3.0S, P. R. Baverstock for valuable criticism, G. B. Sharman, A. Gooley, S. Donnellan, and P. Maiden for invaluable assistance in the field and the Department of Parasitology, University of Queensland, for access to a personal computer and other equipment. This study was supported by grants from the Australian Biological Resources Study to G. B. Sharman and S. C. Barker, an ARGS grant to G. B. Sharman and a Commonwealth Postgraduate Research Award to S. C. Barker.

References

Barker, S. C. (1988). Evolution in the *Heterodoxus octoseriatus* group (Boopiidae: Phthiraptera) and the development of host associattions with *Petrogale* (Marsupialia). Ph.D. Thesis, Macquarie University, North Ryde, N.S.W.

Barker, S. C. (1991*a*). Taxonomic review of the *Heterodoxus octoseriatus* group (Phthiraptera: Boopiidae) from rock-wallabies with the description of three new species. *Systematic Parasitology* **19**, 1–16.

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

Barker, S. C. (1991*c*). Evolution of host–parasite associations among species of lice and rock-wallabies: coevolution? (J. F. A. Sprent Prize Lecture, August 1990.) *International Journal for Parasitology* **21**, 497–501.

Barker, S. C., and Close, R. L. (1990). Zoogeography and host associations of the *Heterodoxus octoseriatus* group and *H. ampullatus* (Phthiraptera: Boopiidae) from rock-wallabies (Marsupialia: *Petrogale*). *International Journal for Parasitology* **20**, 1081–7.

Barker, S. C., Close, R. L., and Briscoe, D. A. (1991*a*). Genetic divergence in *Heterodoxus octoseriatus* (Phthiraptera). *International Journal for Parasitology* **21**, 479–82.

Barker, S. C., Briscoe, D. A., Close, R. L., and Dallas, P. (1991*b*). Genetic variation in the *Heterodoxus octoseriatus* group (Phthiraptera): a test of Price's model of parasite evolution. *International Journal for Parasitology* **21**, 555–63.

Buth, D. B. (1984). The application of electrophoretic data in systematic studies. *Annual Review of Ecology and Systematics* **15**, 501–22.

Clay, T. (1981). A report on a collection of lice (Boopiidae: Phthiraptera) on *Petrogale* (rock wallabies). *Proceedings of the Linnean Society of New South Wales* **105**, 65–78.

Eldridge, M. D. B., Dollin, A. E., Johnston, P. G., Close, R. L., and Murray, J. D. (1988). Chromosomal rearrangements in rock wallabies, *Petrogale* (Marsupialia, Macropodidae). I. The *Petrogale assimilis* species complex: G-banding and synaptonemal complex analysis. *Cytogenetics and Cell Genetics* **48**, 228–32.

Eldridge, M. D. B., Dollin, A. E., Johnston, P. G., Close, R. L., and Murray, J. D. (1989). Chromosomal rearrangements in rock wallabies, *Petrogale* (Marsupialia, Macropodidae). II. G-banding analysis of *P. godmani*. *Genome* **32**, 935–40.

Eldridge, M. D. B., Close, R. L., and Johnston, P. G. (1990). Chromosomal rearrangements in rock wallabies, *Petrogale* (Marsupialia: Macropodidae). III. G-banding analysis of *P. inornata* and *P. penicillata*. *Genome* **33**, 798–802.

Eldridge, M. D. B., Close, R. L., and Johnston, P. G. (1991). Chromosomal rearrangements in rock wallabies, *Petrogale* (Marsupialia: Macropodidae). V. Chromosomal phylogeny of the *lateralis/penicillata* group. *Australian Journal of Zoology* **39**, 629–41.

Nei, M. (1972). Genetic distance between populations. *American Naturalist* **106**, 283–92.

Richardson, B. J., Baverstock, P. R., and Adams, M. (1986). 'Allozyme Electrophoresis.' (Academic Press: Sydney.)

Rogers, J. S. (1972). Measures of genetic similarity and genetic distances. *Studies in Genetics, Volume VII, University of Texas Publication* **7213**, 145–53.

Sharman, G. B., Close, R. L., and Maynes, G. M. (1990). Chromosomal evolution, phylogeny and speciation of rock wallabies (*Petrogale*: Macropodidae). *Australian Journal of Zoology* **37**, 351–63.
Sneath, P. H. A., and Sokal, R. R. (1973). 'Numerical Taxonomy: the Principles and Practice of Numerical Classification.' (W. H. Freeman and Co. Press: San Francisco.)
Swofford, D. L. (1991). 'PAUP: Phylogenetic Analysis Using Parsimony (Version 3.0S).' (Illinois Natural History Survey: Champaign, Illinois, U.S.A.)

Manuscript received 12 March 1991; revised and accepted 18 June 1992