International Journal for Parasitology Vol. 20, No. 8, pp. 1081–1087, 1990
Printed in Great Britain

0020–7519/90 $3.00 + 0.00
Pergamon Press plc

ZOOGEOGRAPHY AND HOST ASSOCIATIONS OF THE *HETERODOXUS OCTOSERIATUS* GROUP AND *H. AMPULLATUS* (PHTHIRAPTERA: BOOPIIDAE) FROM ROCK-WALLABIES (MARSUPIALIA: *PETROGALE*)

STEPHEN C. BARKER* and ROBERT L. CLOSE†

School of Biological Sciences, Macquarie University, New South Wales 2109, Australia

(*Received* 16 *February* 1990; *accepted* 8 *July* 1990)

Abstract—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**: 1081–1087. Species of the *Heterodoxus octoseriatus* group infest five species, comprising eight chromosome races, of *Petrogale* in Queensland and northern New South Wales, Australia. The precise host and geographic ranges of the 11 species of the *H. octoseriatus* group were determined. Individual hosts and host populations were infested by single species of lice only. The geographic ranges of lice were discrete. In some cases the geographic ranges of louse species and their hosts were approximately congruent. In others they were completely incongruent and it was unclear which species originally infested which hosts or even which was the most recent colonizer. In at least one case, expansion of the geographic range of one species of louse apparently led to fragmentation of the range of another and subsequently, to allopatric speciation.

INDEX KEY WORDS:- *Heterodoxus octoseriatus* group; Boopiidae; lice; Phthiraptera; rock-wallaby; *Petrogale*; Marsupialia; zoogeography; parapatry; speciation; host associations; Queensland, Australia; infestation; host switching.

INTRODUCTION

ROCK-WALLABIES (*Petrogale* spp.) inhabit rocky gorges, boulder outcrops and cliffs throughout mainland Australia. These macropodid marsupials are infested by species of lice of the *Heterodoxus octoseriatus* and *H. ampullatus* groups (Clay, 1981; Barker, in press a). Previous collections of lice (see Clay, 1981; von Kéler, 1971) have been small and largely incidental to host studies. In this paper the geographic and host ranges of the 11 species of the *H. octoseriatus* group and *H. ampullatus* are determined for the first time. Particular attention was paid to the margins of parasite ranges and regions of parapatry between hosts infested with different species of lice.

Accurate determination of the geographic and host ranges of parasites is important because it: (i) will allow the host–parasite coevolution model to be tested and trends in the evolution of host–parasite associations to be identified; (ii) may provide insight into the evolution of host and parasite groups; and (iii) may provide insight into the ecology and in particular the interspecific relationships of the lice.

* Present address and address for correspondence: Department of Parasitology, University of Queensland, St. Lucia, Queensland 4067, Australia.

† Present address: School of Business and Technology, University of Western Sydney, Macarthur, Campbelltown, New South Wales 2560, Australia.

MATERIALS AND METHODS

Rock-wallabies were identified to chromosome race and species by karyotypic examination (Briscoe, Calaby, Close, Maynes, Murtagh & Sharman, 1982; see also Sharman, Close & Maynes, 1990). The genus *Petrogale* comprises 19 chromosome races which were grouped into 10 provisional species by Briscoe *et al.* (1982). Subsequently, the *assimilis* chromosome race was removed from *P. inornata* to *P. assimilis* (see Calaby & Richardson, 1988), and the Cape York race from *P. godmani* to a separate, but as yet unnamed species (Eldridge, Johnson, Close & Lowry, 1989). Thus, at present the 19 chromosome races are grouped into 12 species. This study involves eight chromosome races grouped into five species, which occur in eastern Australia (Figs. 2–5). Two hundred and eleven hosts were made available to us from a separate study of evolution in the genus *Petrogale* (Tables 1–3). Lice were collected with forceps from hosts in the field, and washed from host skins held in separate containers of 70% alcohol. A strong jet of water dislodged lice from host fur and a 180 μm filter collected nymphs and adults. One to 18 adult lice were examined from individual hosts and were identified to species following Clay (1981) and Barker (in press a). The geographic ranges of louse species were inferred from maps on which a line was drawn around the known localities of each species.

RESULTS AND DISCUSSION

Zoogeography and host associations

Each of the 211 host individuals and all rock-wallabies collected at each locality were infested by single species of lice only (Tables 1–3). Comparison with other phthirapteran groups is hampered by the *ad hoc* nature of most collections; few contain specimens from all or even most parts of the geographic ranges of hosts. Further, host–parasite check-lists focus on the lice collected from host species rather than host

TABLE 1—COLLECTIONS OF *Heterodoxus ampullatus*, *H. octoseriatus*, *H. maynesi* AND *H. briscoei* EXAMINED FROM *Petrogale* TAXA

	Host number(s)		Latitude	Longitude
		Heterodoxus ampullatus		
		ex *P. p. penicallata*		
1	S715–6	Grampians Victoria	37°18′S	142°33′E
2	B193–207	Jenolan Caves NSW	33°49′S	150°02′E
3	82–130	Watagan State Forest NSW	37°00′S	151°19′E
		H. octoseriatus		
		ex *P. p. penicallata*		
4	S523	Gorge Ck Bonalbo NSW	28°45′S	152°42′E
5	RW10,RW11	Emu Vale	28°13′S	152°15′E
6	S688	Nukinenda Falls Bearkin	27°00′S	152°10′E
7	S671	Perseverance Dam	27°17′S	152°07′E
8	S679, S681–2	Cooyar Ck Noora Stn	26°49′S	152°04′E
		ex *P. p. herberti*		
9	S676, RW16	*Yarraman Ck	26°47′S	152°03′E
10	S689	Taromeo Ck Tellah Stn	26°47′S	152°08′E
11	S684	Round Scrub Tuckerimbah Stn	26°45′S	152°10′E
12	S678	Kinbombi Falls Goomeri	26°13′S	152°09′E
13	S451–2	Kilmorey Stn	26°05′S	148°11′E
14	RW26–7	Cania Gorge	24°41′S	150°58′E
15	S456, S457/S458, S885/S886	Mt Sebastopol Stn	23°39′S	150°09′E
16	RW35	Mt Ball	23°19′S	147°40′E
17	S466	Fitzroy R Armagh Stn	23°17′S	149°50′E
		ex *P. inornata*		
18	S462	Pine Mountain	23°11′S	150°37′E
19	S460	Mt Nicholson	23°20′S	150°37′E
		H. maynesi		
		ex *P. p. herberti*		
21	S455	Sequens	23°58′S	149°45′E
22	S453/S454	Mt Sirloin Arduran Stn	23°50′S	148°57′E
		ex *P. inornata*		
24	S739	Emu Plains Stn	20°48′S	148°03′E
25	S744	Pelican Ck Myuna Stn	20°36′S	147°41′E
26	S463/S465	4 Mile Ck Boomer Range	23°14′S	149°49′E
27	RW158, RW164, RW166–7	Apis Creek Stn	23°01′S°	149°34′E
28	S467	Isaacs R Gorge Burton Downs Stn	21°39′S	148°07′E
29	RW146–8, RW152–3, RW155	Blue Mountain Wandoo Stn	21°32′S	149°08′E
30	S871–2	Sawmill Beach Whitsunday Is.	20°16′S	148°57′E
31	B119	Dugong Beach Whitsunday Is.	20°15′S	148°57′E
32	S713	Joe's Beach Whitsunday Is.	20°16′S	148°56′E
33	S649A	Mt Johnnycake Blue Valley Stn	20°25′S	147°24′E
34	RW136–8	Guthulungra	19°56′S	147°52′E
35	S692,S694	Flagstaff Bay	19°46′S	147°46′E
36	S644	Mt Louisa Bryne Valley Stn	19°53′S	147°14′E
37	S648	Gregory Range Byrne Valley Stn	19°56′S	147°19′E
38	S735	Lowestoft Stn	22°52′S	148°11′E
		H. briscoei		
		ex *P. p. herberti*		
40	S736–7	Mt Donnybrook Laglan Stn	22°31′S	146°44′E
41	S733	Lestree Hill Trelawney Stn	22°50′S	146°42′E

(–) indicates separate louse collections were made from hosts with consecutive collection numbers; (/) indicates lice from two hosts were pooled.

* *P. p. penicillata* captured at this site also (unpublished data).

All localities in Queensland, except where indicated. Column 1 is site number and column 3 is locality.

TABLE 2—COLLECTIONS OF *Heterodoxus insulatus*, *H. lesouefi*, *H. harrisoni*, *H. hughendensis*, *H. closei* AND *H. insularis* EXAMINED FROM *Petrogale* TAXA

	Host number(s)		Latitude	Longitude
		H. insulatus		
		ex *P. a. assimilis*		
42	B58–59	Maud Bay Magnetic Is.	19°07′S	146°50′E
43	S879	Cape Cleveland	19°11′S	147°01′E
44	S874	Cape Ferguson	19°17′S	147°04′E
45	B148–9	Alma Bay Magnetic Is.	19°09′S	146°52′E
46	ANIC	Magnetic Is.		
		H. lesouefi		
		ex *P. a. assimilis*		
47	469	Mt Helena Natal Downs Stn	21°04′S	146°16′E
48	470	The Pinnacles Charters Towers	20°08′S	146°15′E
49	S728	White Mtn Ck Goldsborough Stn	20°22′S	144°53′E
50	S724, S726	Humpy Ck Clyde Park Stn	20°24′S	144°40′E
51	S732	Lolworth Stn	20°11′S	145°01′E
52	S721–2, RW291, RW293	Porcupine Gorge	20°21′S	144°27′E
53	S607, S609	Porcupine Gorge Boonderoo Stn	20°18′S	144°30′E
54	S905	Horse Mtn Lyndhurst Stn	19°11′S	144°20′E
55	S906, RW90	16 km S of Lyndhurst Stn	19°20′S	144°20′E
		H. harrisoni		
		ex *P. a. assimilis*		
56	S902	Maiden Springs Stn	19°54′S	144°03′E
57	RW85, B172–4, B179, S913–4	Black Rock Lyndhurst Stn	19°05′S	144°27′E
58	S922	Watch Hill Watch Hill Stn	19°02′S	144°32′E
59	S701	Newcastle Range	18°19′S	143°41′E
60	S697–9	Ironhurst Stn	17°59′S	143°27′E
		ex *P. assimilis* Mareeba		
61	RW298	Mungana Trucking Yard	17°06′S	144°23′E
		H. hughendensis		
		ex *P. a. assimilis*		
63	S601–2	Betts Gorge Torver Valley Stn	20°40′S	144°07′E
64	S603, S605	Spring Lawn Ck Boonderoo Stn	20°23′S	144°21′E
65	S727	Galah Ck S of Porcupine Gorge	20°29′S	144°24′E
		H. closei		
		ex *P. a. assimilis*		
67	S625, S628, S630, S878	The Pyramids Alehvale Stn	18°13′S	142°22′E
		H. insularis		
		ex *P. inornata*		
70	S740	W of Bald Hill Havilah Stn	20°54′S	147°48′E
		ex *P. a. assimilis*		
71	S743	Frederick Ck Birralee Stn	20°43′S	147°38′E
72	S741	Glenmore Ck Myuna Stn	20°35′S	147°34′E
73	S650, S652	Mt Wicklam Stn	20°30′S	147°28′E
74	S477/S479	The Twins Mt Cooper Stn	20°30′S	146°59′E
75	S473/S475	Mt Robbins Mt Cooper Stn	20°35′S	146°58′E
76	S614	Mt Dalrymple Landers Ck Stn	19°59′S	147°13′E
77	S611–2	Hillsborough Stn	20°07′S	147°03′E
78	S425–6	10 km W of Tabletop Stn	19°26′S	146°24′E
79	82–140, 84–004	Tabletop Stn	19°23′S	146°28′E
80	B56	Hervey Range Rd	19°23′S	146°28′E
81	82–141 to 82–143, B00, B000	Mt Stuart Townsville	19°21′S	146°47′E
82	S851-2	Mt Fullstop	19°11′S	145°33′E
84	S853, S856	Tomahawk Ck Kangaroo Hills Stn	19°04′S	145°41′E
85	S481, S483/S484	Expedition Ck Blue Range Stn	19°07′S	145°29′E
86	RW127	Onion Bay Great Palm Is.	18°46′S	146°36′E
87	RW125	Munday Bay Great Palm Is.	18°46′S	146°37′E
88	S631–2	Glenlofty Ck Valley of Lagoons Stn	18°35′S	145°08′E
89	RW325	Reedy Brook Stn	18°41′S	145°05′E
		ex *P. assimilis*-Mt Claro		
83	S854–5	Biscuit Ck Kangaroo Hills Stn	19°02′S	145°43′E

Continued

TABLE 2 *continued*

	Host number(s)		Latitude	Longitude
91	S424	Lincoln Springs Stn	18°41′E	145°30′E
92	S633–5,S860	Mt Claro	18°52′S	145°44′E
		ex *P. assimilis*-Mareeba		
90	S876	Mt Garnet/Innot Hot Springs	17°45′S	145°11′E
93	S486–7	Glen Harding Stn	18°15′S	145°07′E
94	B139–40	Tinaroo Falls Barron R	17°10′S	145°30′E
95	S333, S335	Mt Aunt	17°05′S	145°23′E
96	S615	Southedge Stn	16°50′S	145°12′E

(–) indicates separate louse collections were made from hosts with consecutive collection numbers; (/) indicates lice from two hosts were pooled.

All localities in Queensland. Column 1 is site number and column 3 is locality.

TABLE 3—COLLECTIONS OF *Heterodoxus murrayi* AND *H. orarius* EXAMINED FROM *Petrogale* TAXA

	Host number(s)		Latitude	Longitude
		H. murrayi		
		ex *P. assimilis*-Mareeba		
101	S930	Mitchell R Bellevue Stn	16°30′S	144°09′E
102	S928	Mitchell R Bellevue Stn	16°30′S	144°10′E
104	S703-4	Walsh R Blackdown Telegraph Stn	16°53′S	143°57′E
107	RW315, RW319, S322, S875	Mt Alto	16°34′S	145°06′E
		ex *P. godmani*		
100	S506, S508, S510	Mt Elephant	16°29′S	144°55′E
106	S618–9	Church Hill Curraghmore Stn	16°29′S	145°02′E
105	S501–2, S390, S616–7	Dingo Hill Brooklyn Stn	16°30′S	145°01′E
		ex *P. godmani–P. assimilis*-Mareeba hybrid		
105	S620	Dingo Hill Brooklyn Stn	16°30′S	145°01′E
		ex Cape York species		
108	RW100	14 km NE of Coen	13°50′S	143°08′E
109	S868	Fall Ck Pascoe R	12°56′S	143°02′E
		H. orarius		
		ex *P. godmani*		
111	S927	Mt Mulgrave	16°13′S	144°02′E
112	S929	Mitchell R Mt Mulgrave Stn	16°26′S	144°08′E
113	S705	Fairlight Stn	15°47′S	144°03′E
114	S924–5	Pinnacle Stn	15°44′S	143°34′E
115	RW94–5,RW97	Byerstown Range	15°57′S	144°50′E
116	S621–2	Mt McDonald Kings Plains Stn	15°42′S	145°01′E
117	S511	Laura	15°39′S	144°32′E
118	S623	Black Mtn/Annan R Gorge	15°41′S	145°12′E
120	S657, S659–61	Bathurst Head	14°18′S	144°13′E
		ex Cape York species		
119	S865–6	Edward River Rd Artemis Stn	14°48′S	143°26′E

(–) indicates separate louse collections were made from hosts with consecutive collection numbers.
All localities in Queensland. Column 1 is site number and column 3 is locality.

individuals. Nonetheless, for the chewing or biting lice (Amblycera and Ischnocera) of mammals it is apparently uncommon to find more than one species on an individual host (Timm, 1983). Species of the *Heterodoxus octoseriatus* group infest at least five species, comprising eight chromosome races, of *Petrogale* (Tables 1–3).

The geographic ranges of the 11 species of the *H. octoseriatus* group were discrete. Many were parapatric, some were allopatric: none was sympatric (Fig. 1).

Two louse species infested *P. p. penicillata*: *H. ampullatus* throughout at least half of its known range and *H. octoseriatus* adjacent to the *P. p. penicillata–P. p. herberti* contact zone (Fig. 2). The simplest explanation for these associations is that host switching has occurred. *H. octoseriatus* from *P. p. herberti* apparently colonized *P. p. penicillata* [a *P. p. penicillata–P. p. herberti* hybrid zone exists near Nanango,

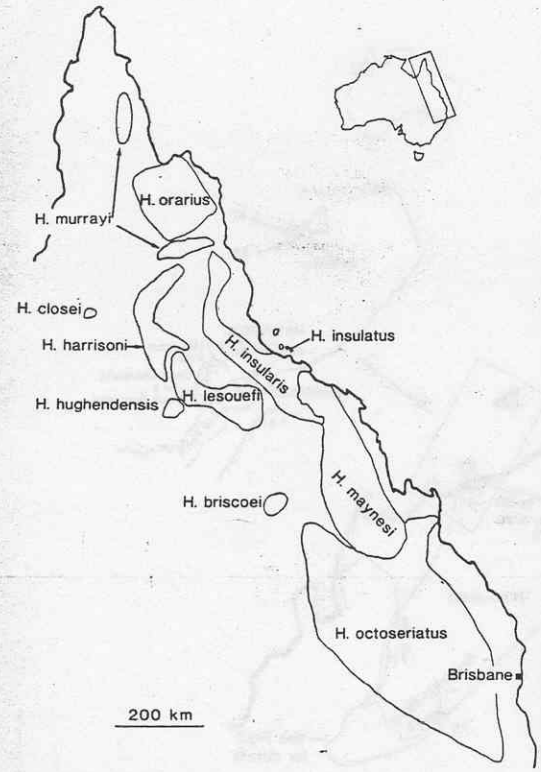

FIG. 1. Geographic ranges of louse species of the *Heterodoxus octoseriatus* group in north-eastern Australia.

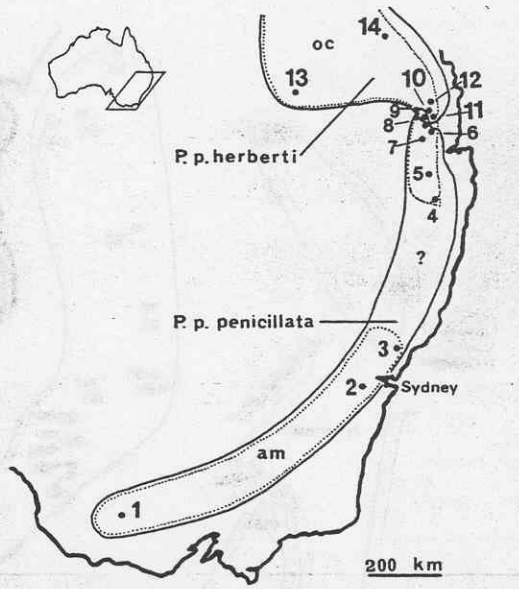

FIG. 2. Geographic and host ranges of *Heterodoxus ampullatus* (am) and *Heterodoxus octoseriatus* (oc) (southern section). Dotted lines: geographic ranges of louse species; solid lines: geographic ranges of *Petrogale* taxa, site numbers from Table 1.

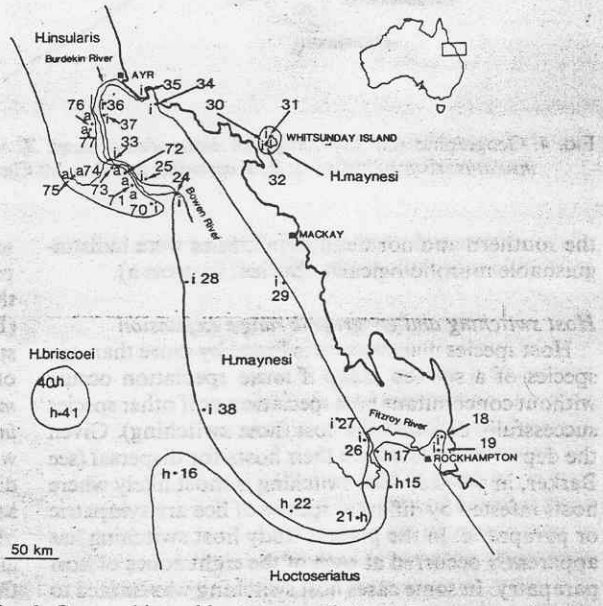

FIG. 3. Geographic and host ranges of *Heterodoxus maynesi* and zones of parapatry with *H. octoseriatus* and *H. insularis*. Key to hosts—h: *Petrogale p. herberti*; i: *P. inornata*; a: *P. a. assimilis*; site numbers from Tables 1, 2.

west of Brisbane (Briscoe *et al.*, 1982)]. *H. octoseriatus* apparently then spread at least 225 km into the former range of *H. ampullatus*. Alternatively, *H. octoseriatus* formerly infested *P. p. penicillata*, throughout its range. Having colonized *P. p. penicillata* from an unknown host, *H. ampullatus* expanded its geographic range to the point where it now infests *P. p. penicillata* throughout at least half of the 1000 km north–south geographic range of this rock-wallaby.

The geographic ranges of *P. inornata* and *H. maynesi* were congruent except at their southern and northern boundaries (Fig. 3). The simplest explanation for these associations is that host switching occurred where the geographic ranges of *P. inornata* and *H. maynesi* abut with those of *P. p. herberti* and *H. octoseriatus* in the south, and with *P. a. assimilis* and *H. insularis* in the north.

The three chromosome races that constitute *P. assimilis* were infested by seven louse species: *H. lesouefi*, *H. hughendensis*, *H. harrisoni*, *H. closei*, *H. insularis*, *H. insulatus* and *H. murrayi* (Figs. 4,5). It is unclear which of these species originally infested *P. assimilis* (*sensu stricto*), and the races *P. assimilis*-Mareeba and *P. assimilis*-Mt Claro.

H. murrayi comprised two groups of populations which were separated by up to 300 km (Fig. 5). The simplest explanation for this division of *H. murrayi* is that a westward expansion of *H. orarius* bisected a once continuous distribution of *H. murrayi*. This expansion was probably recent since *H. murrayi* from

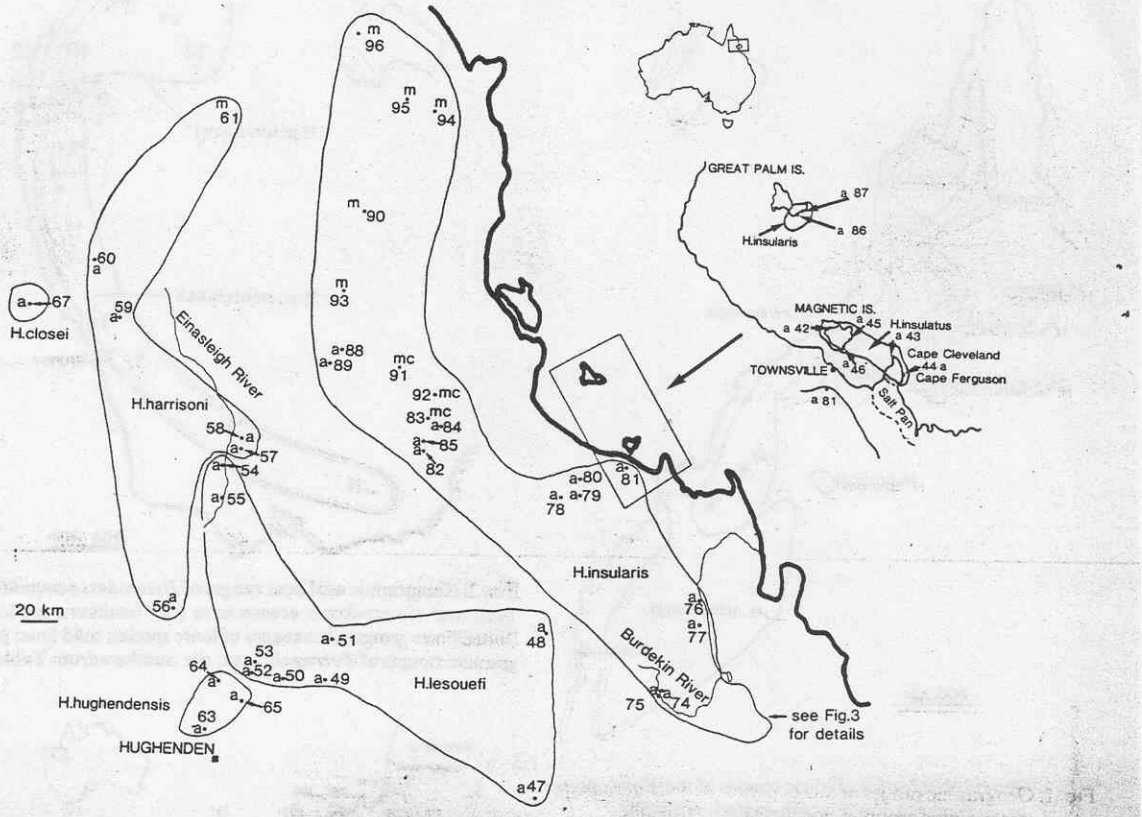

FIG. 4. Geographic and host ranges of *Heterodoxus closei*, *H. harrisoni*, *H. hughendensis*, *H. lesouefi*, *H. insularis* and *H. insulatus*. Key to hosts—a: *P. a. assimilis*; mc: *P. a.* Mt Claro; m: *P. a.* Mareeba; site numbers from Tables 2, 3.

the southern and northern populations were indistinguishable morphologically (Barker, in press a).

Host switching and geographic range expansion

Host species may become infested by more than one species of a species group if louse speciation occurs without concomitant host speciation or if other species successfully colonize the host (host switching). Given the dependence of lice on their hosts for dispersal (see Barker, in press b) host switching is most likely where hosts infested by different species of lice are sympatric or parapatric. In the present study host switching has apparently occurred at each of the eight zones of host parapatry. In some cases host switching was limited to the zone of parapatry (between *P. p. herberti* and *P. inornata*, and *P. inornata* and *P. a. assimilis*). Other louse species apparently have expanded their geographic range well beyond the host contact zone, to the point where it is unclear which louse species was the original or even the most recent colonizer, e.g. the six species which infest *P. a. assimilis* (Fig. 4).

In at least one case, expansion of the geographic range of one species of louse apparently led to fragmentation of the range of another and subsequently, to allopatric speciation. A phylogeny predicted from morphological characters indicates that *H. orarius* and *H. insularis* are sister species (Barker, in press b). The geographic ranges of these species are separated by part of the geographic range of *H. murrayi* (Figs. 1, 5). Thus, range expansion by *H. murrayi* may have fragmented the *H. orarius–H. insularis* ancestor leading to speciation. In a similar way range expansion by *H. orarius* apparently has dissected the geographic range of *H. murrayi* into separated allopatric groups of populations. Analysis of morphological characters (Barker, in press a) and allozymes at seven loci (Barker, unpublished Ph.D thesis, Macquarie University, 1988) indicate that these have not speciated. However, if isolation persists speciation may occur. Thus, in a novel way, host switching and expansion of the geographic ranges of louse species may lead to speciation.

Acknowledgements—We thank: M. D. Murray, D. A. Briscoe and G. B. Sharman for valuable discussion—G. B. S. also collected some hosts; A. Gooley, J. Middleton, J. Stevens, R. Delaney and S. Donnellan for enthusiastic and expert assistance in the field; the Queensland, NSW and

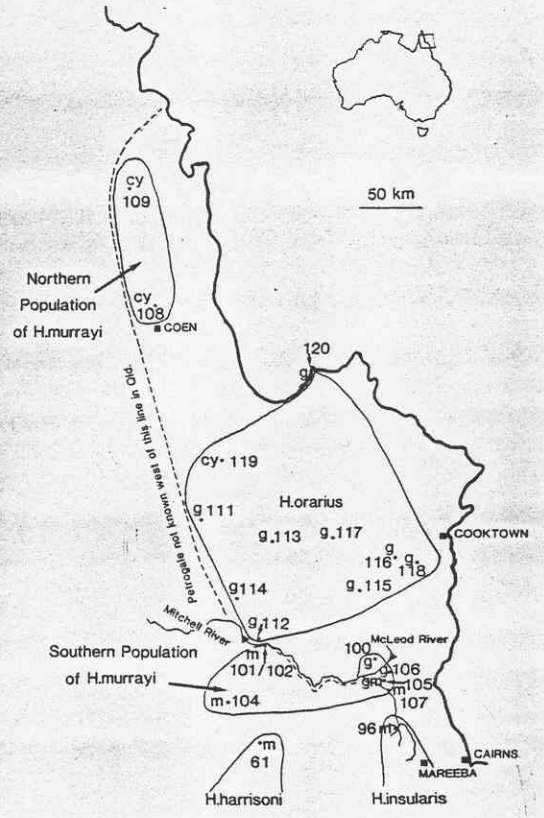

FIG. 5. Geographic and host ranges of *Heterodoxus murrayi* and *H. orarius*. Key to hosts—cy: Cape York species (unnamed); g: *P. godmani*; m: *P. assimilis* Mareeba; site numbers from Table 3.

Victorian fauna authorities for permits to trap and collect rock-wallabies; and M. D. Murray, D. M. Spratt, I. D. Whittington and D. S. Kettle for criticizing earlier drafts.

This project was supported by an Australian Biological Resources Study grant and a Commonwealth Postgraduate Research Award to S. C. B.

REFERENCES

BARKER S. C. (in press a) Taxonomic review of the *Heterodoxus octoseriatus* group (Phthiraptera: Boopiidae) with the description of three new species. *Systematic Parasitology*.

BARKER S. C. (in press b) Phylogeny of the *Heterodoxus octoseriatus* group (Phthiraptera: Boopiidae) from rock-wallabies (Marsupialia: *Petrogale*). *Systematic Parasitology*.

BRISCOE D. A., CALABY J. H., CLOSE R. L., MAYNES G. M., MURTAGH C. E. & SHARMAN G. B. 1982. Isolation, introgression and genetic variation in rock-wallabies. In: *Species at Risk: Research in Australia* (Edited by GROVES R. H. & RIDE W. D. L.), pp. 73–87. Australian Academy of Science, Canberra.

CALABY J. H. & RICHARDSON B. J. 1988. Macropodidae. In: *Zoological Catalogue of Australia*, Vol. 5, *Mammalia* (Edited by WALTON D. W.), pp. 60–80. Australian Government Publishing Service, Canberra, Australia.

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

ELDRIDGE M. D. B., JOHNSTON P. G., CLOSE R. L. & LOWRY P. S. 1989. Chromosomal rearrangements in rock wallabies, *Petrogale* (Marsupialia: Macropodidae). II. G-banding analysis of *Petrogale godmani*. *Genome* **32**: 935–940.

KÉLER S. VON 1971. A revision of the Australasian Boopiidae (Insecta: Phthiraptera) with notes on the Trimenoponidae. *Australian Journal of Zoology*, Supplementary Series **6**: 1–126.

SHARMAN G. B., CLOSE R. L. & MAYNES G. M. 1990. Chromosome evolution, phylogeny and speciation of rock wallabies (*Petrogale*: Macropodidae). *Australian Journal of Zoology* **37**: 351–363.

TIMM R. M. 1983. Fahrenholz's rule and resource tracking: a study of host–parasite coevolution. In: *Coevolution* (Edited by NITCKI M. H.), pp. 225–265. University of Chicago Press, Chicago.