Systematic Parasitology **44:** 79–85, 1999.

Have chondracanthid copepods co-speciated with their teleost hosts?

Adrian M. Paterson[1] & Robert Poulin[2]
[1]*Ecology and Entomology Group, Lincoln University, PO Box 84, Lincoln, New Zealand*
[2]*Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand*

Accepted for publication 26th October, 1998

Abstract

Chondracanthid copepods parasitise many teleost species and have a mobile larval stage. It has been suggested that copepod parasites, with free-living infective stages that infect hosts by attaching to their external surfaces, will have co-evolved with their hosts. We examined copepods from the genus *Chondracanthus* and their teleost hosts for evidence of a close co-evolutionary association by comparing host and parasite phylogenies using TreeMap analysis. In general, significant co-speciation was observed and instances of host switching were rare. The prevalence of intra-host speciation events was high relative to other such studies and may relate to the large geographical distances over which hosts are spread.

Introduction

About one-third of known copepod species are parasitic on invertebrates or fish (Humes, 1994). The general biology of copepods parasitic on fish is much better known than that of copepods parasitic on invertebrates (Kabata, 1981). Apart from a handful of exceptions, all copepods parasitic on fish have direct, one-host life-cycles. Adults live attached to the external surfaces (skin, fins, gills, nares, buccal cavity) of fish. Females produce egg-sacs containing anywhere from a few hundred to several thousand eggs. These hatch into nauplii, which are free-swimming, non-feeding larvae. The nauplius then moults into a copepodid which, upon contact, infects a suitable host. The adult stage follows a few additional moults, e.g. typically the copepodid metamorphoses into an adult gradually over several moults. Males are usually dwarfs relative to females; they attach to females to transfer spermatophores, and often die after copulating.

The family Chondracanthidae de Blainville, 1822 contains about 160 species, all parasitic on marine fish (Ho, 1991). The genus *Chondracanthus* Delaroche, 1811 is one of the most speciose in the family. It contains 37 valid species (Ho, 1991) known from 66 marine fish species belonging to 26 families and 9 orders. Twenty-two species of *Chondracanthus* are known from the Pacific, and 17 species from the Atlantic (2 species occur in both oceans; none are reported from the Indian Ocean).

Parasites with direct life-cycles, as well as parasites with free-living infective stages that infect hosts by attaching to their external surfaces, are often said to (i) have a narrower range of suitable host species and (ii) have co-evolved with their hosts more closely than parasites with indirect life-cycles and/or transmission by ingestion (Noble et al., 1989). Copepods have direct life-cycles with a free-living stage and are often considered to be very host specific (Kabata, 1981). Comparative data on many copepod species are difficult to obtain, but what is available does not support this general claim (Poulin, 1992). Monogeneans, another group of metazoan ectoparasites of fish with direct life-cycles, show agreement with the above prediction and are truly very host specific (Poulin, 1992). Almost no work has been done on the co-evolution question apart from three studies on copepods which indicated some broad coevolutionary patterns (Dojiri & Deets, 1988: Sphyriidae; Deets & Ho, 1988: Eudactylinidae; Deets, 1994: chondrichthyan – copepod).

The present-day distribution of any parasite species on host species is the result of an interplay of processes that determine the presence or absence of a parasite from a given host. Parasites may be present because of an association with the ancestors of the host or because the parasite's ancestors have host switched from another host lineage (Brooks & McLennan, 1991). If parasites have been passed down through the host's lineage then they have co-speciated and we might expect to see evidence of this if we compare host and parasite phylogenies, i.e. they will be significantly congruent (Page, 1990; Paterson & Gray, 1997). Host switching by parasites will disrupt this signal. So looking for co-speciation, and other co-evolutionary events, between host and parasite becomes a matter of testing for significant congruence between their phylogenies.

There are several different events that can occur in a co-evolutionary relationship. For example, parasites may speciate with their hosts (co-speciation), speciate without their host (intra-host speciation), go extinct (sorting) and move from one lineage to another (host switching). TreeMap is a program developed to test for these co-evolutionary events working on the assumption of maximising the number of co-speciation events (Page, 1994). In this paper we use TreeMap analysis to examine whether copepods of the genus *Chondracanthus* and their teleost hosts have co-evolved.

Materials and methods

Data were collected on the phylogenies of various marine teleost fish orders (Nelson, 1994: Gadiformes, Ophidiiformes, Pleuronectiformes, Scorpaeniformes, Zeiformes) for which there was good phylogenetic information on their copepod parasites from the genus *Chondracanthus* (see Ho, 1991 and Table I). A further host unit ('representatives') was created by selecting members of each of the five orders for which a reasonable amount of life-history information is known (Figure 1).

TreeMap (Page, 1994), a type of component analysis, was used to examine all possible host switching scenarios. TreeMap achieves this by mapping the parasite phylogeny onto the host phylogeny given the distribution of parasite between host species. TreeMap then selects the outcome(s) that maximises the number of co-speciation events. The maximum number of co-speciation events found was then assessed for significance against a null distribution of co-speciation events generated by randomising the host phylogeny.

Results

The TreeMap analysis provided support for co-speciation of copepods and their fish hosts in the orders Ophidiiformes, Pleuronectiformes, Scorpaeniformes and Zeiformes. There was no support for co-speciation in the Gadiformes (Table II, Figure 2). The representatives provided ambiguous results. This was because there was a three-way polytomy which could be resolved in three ways. There was significant co-speciation in topology A, *C. australis* and allies as the most basal branch, if one episode of host switching was allowed, *C. theragrae*, etc, as the most basal was significant (topology B), and with *C. psetti* and *C. janebennettae* as the most basal was not significant (topology C).

Both analyses of the Ophidiiformes and Scorpaeniformes indicated that the common ancestors of the genera included already possessed most of the lineages found on extant species. Only two likely instances of host switching were observed. The first involved the species *C. pinguis*. In the Scorpaeniformes *C. pinguis* has switched from *Dasycottus* to *Sebastes.* The second host switching event was detected in the representative analysis where a population of the ancestor of *C. triventricosus* has colonised the Gadiformes and radiated to become *C. theragrae*.

Discussion

Although copepods have low levels of host specificity (Poulin, 1992), it appears, at least for the *Chondracanthus* group, that they do show significant co-evolution within fish orders. There may be higher level patterns, as suggested by the ambiguous results of the representatives analysis. Outside of the Gadiformes host switching appeared to occur only infrequently. Of the five orders looked at in this analysis, the Gadiformes (cods and their allies) are the least benthic. Perhaps broadcasting larvae in the water column provides more opportunities for host switching than swimming close to the substrate? Outside of the Gadiformes, host switching does not appear to have played a major role within the genus *Chondracanthus*. This is surprising in an organism with a free-living and motile stage. What prevents copepods from colonising other potential host species in an area? Larvae are small and cannot move great distances, which may limit the value of free-living dispersal. Competitive exclusion is probably

Table I. *Chondracanthus* spp. and their teleost host genera used in this study.

Parasite species	Host genera
C. australis Ho, 1991	*Merluccius* Rafinesque
C. barnardi Go, 1972	*Lophius* Linnaeus
C. brotulae Capart, 1959	*Molva* LeSueur, *Brotula* Cuvier
C. colligens Barnard, 1955	*Genypterus* Philippi
C. cotunculi Rathbun, 1886	*Cottunculus* Collett
C. distortus Wilson, 1922	*Zeus* Linnaeus, *Cottus* Linnaeus
C. genypteri Thomson, 1889	*Genypterus* Philippi
C. irregularis Fraser, 1920;	*Myoxocephalus* Tilesius
C. janebennettae Causey, 1953	*Ancylopsetta* Gill
C. lepophidii Ho, 1974	*Lepophidium* Gill
C. lophii Johnston, 1836	*Lophius* Linnaeus
C. merlucci (Holten, 1802)	*Merluccius* Rafinesque
C. multituberculatus (Markewitsch, 1956)	*Dasycottus* Bean
C. neali Leigh-Sharpe, 1930	*Malacephalus* Günther
C. nodosus (Müller, 1777)	*Sebastes* Cuvier
C. palpifer Wilson, 1912	*Merluccius* Rafinesque
C. pinguis Wilson, 1912	*Sebastes* Cuvier
C. polymixiae Yamaguti, 1939	*Polymixia* Lowe
C. psetti Kroyer, 1836	*Pleuronectes* Linnaeus, *Paralichthys* Girard
C. quadratus (Heegaard, 1945)	*Diodon* Linnaeus
C. shiinoi (Shiino, 1955)	*Zenion* Jordan & Evermann
C. theragrae Yamaguti, 1939	*Theragra* Lucas
C. triventricosus Sekerak, 1970	*Sebastes* Cuvier
C. tuberculatus Nordmann, 1832	*Congiopodus* Perry
C. yanezi Atria, 1980	*Neophrinichthys* Günther, *Psychrolutes* Günther
C. zei Delaroche, 1811	*Zenopis* Gill

Table II. Results of the TreeMap analyses between the phylogenies of *Chondracanthus* spp. and various fish orders. Number of co-speciation (C), intra-host speciation (I), host switching (H) and sorting (S) events found in the maximum co-speciation tree are shown. The distribution of maximum co-speciation values from TreeMap analysis of 100 randomised host trees are shown.

Host order	Maximum co-speciation				Randomised co-speciation distribution				
	C	I	H	S					
Gadiformes	2	3	0	3	0-0	1-76	2-24		P = 0.24
Ophidiiformes	2	3	0	7	0-54	1-45	2-1		P = 0.01
Pleuronectiformes	1	1	0	2	0-100				P<0.01
Scorpaeniformes	4	3	1	13	0-0	1-65	2-32	3-3	P<0.01
Zeiformes	2	1	0	1	0-100				P<0.01
Representatives:									
Topology A	3	5	1	9	0-0	1-66	2-30	3-4	P = 0.04
Topology B	3	6	0	16	0-0	1-55	2-44	3-1	P = 0.01
Topology C	2	7	0	18	0-0	1-34	2-60	3-6	P = 0.66

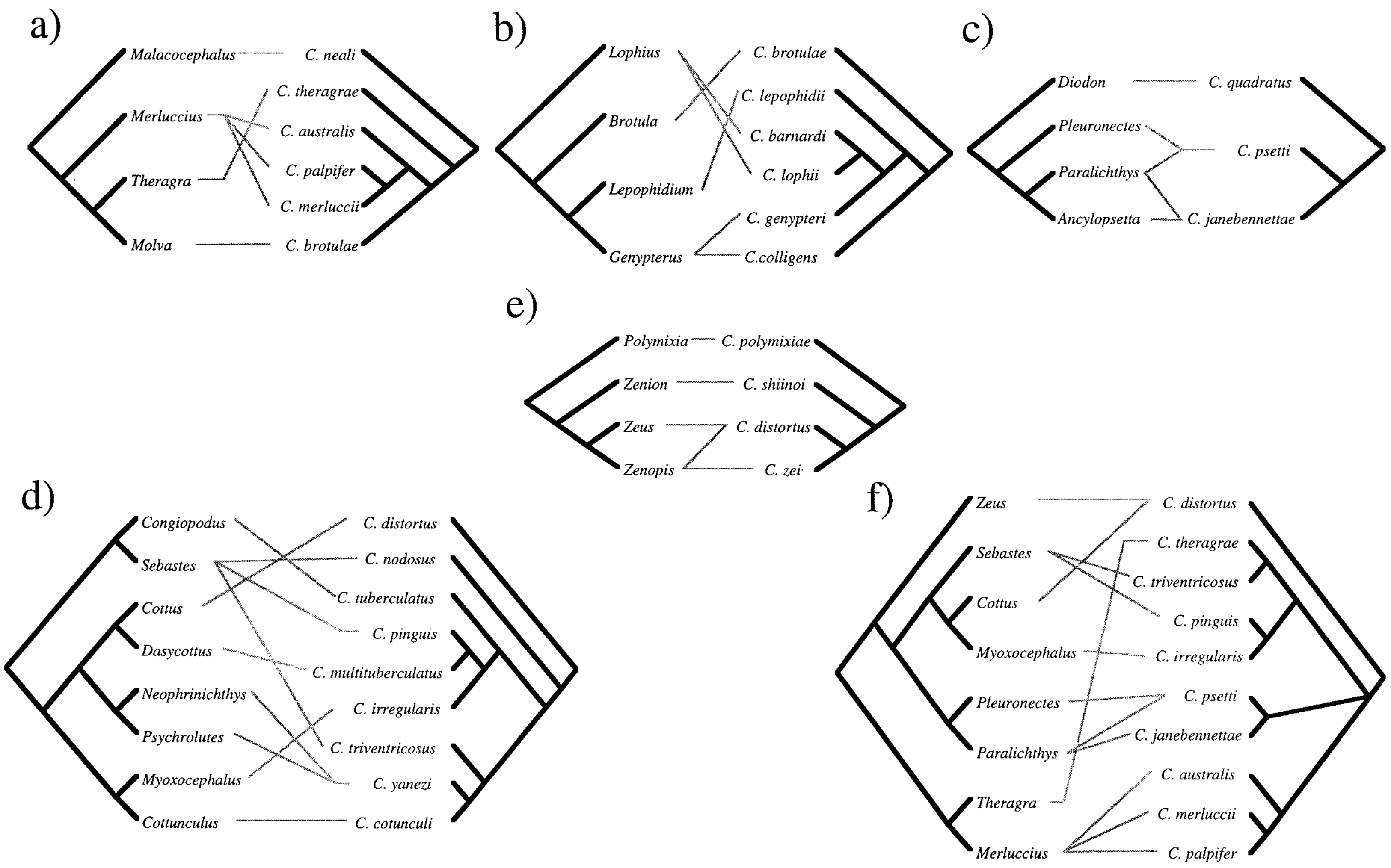

Figure 1. Tanglegrams of fish (left) and copepod (right) phylogenies showing the distribution of each copepod species (grey line) for (a) Gadiformes, (b) Ophidiiformes (and Lophiiformes outgroup), (c) Pleuronectiformes (and Tetraodontiformes outgroup), (d) Scorpaeniformes, (e) Zeiformes (and Beryciformes outgroup) and (f) representatives from the various fish orders.

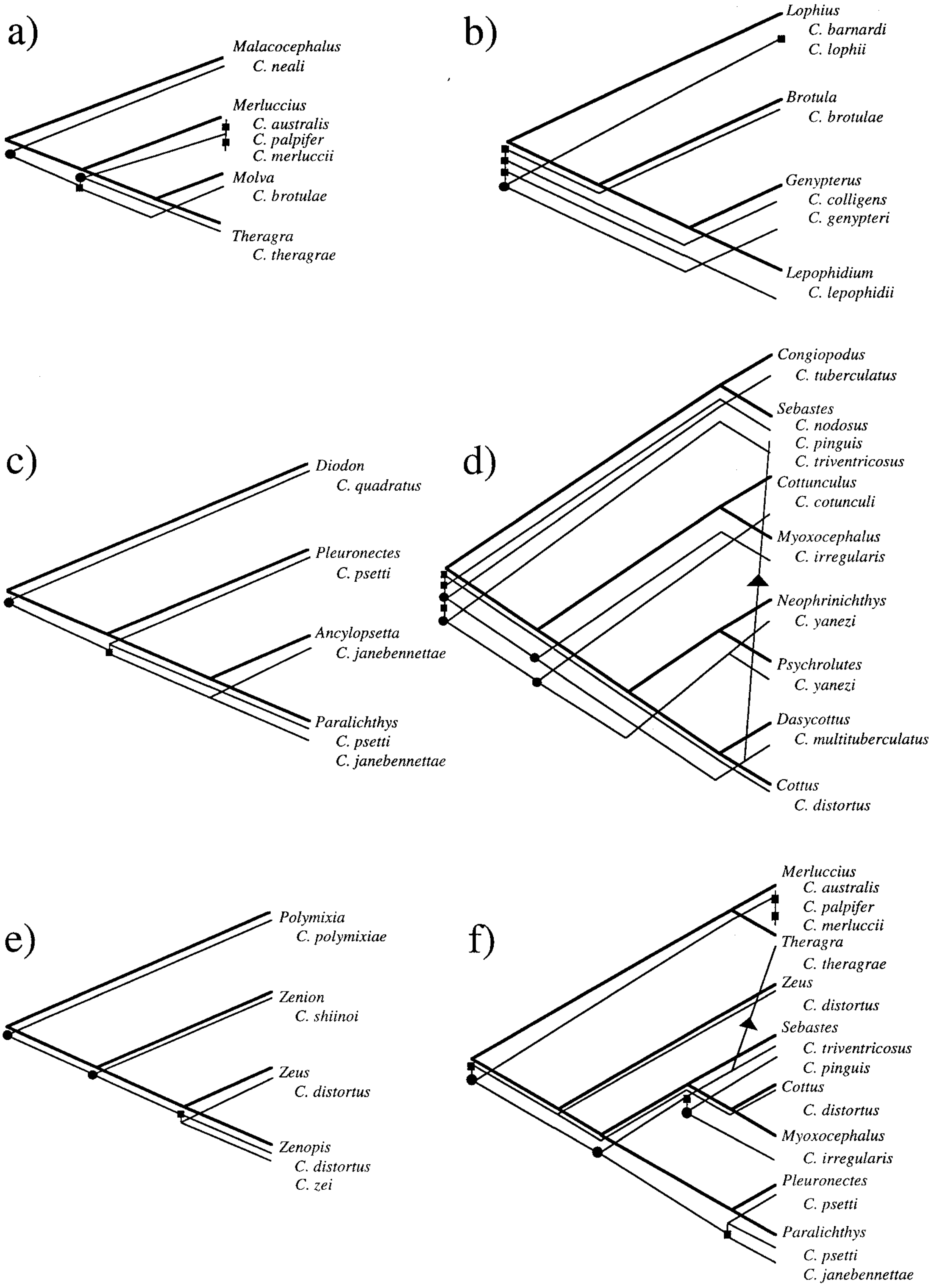

Figure 2. Stacked TreeMap reconciliation trees of fish phylogeny (thick lines) with the maximum co-speciation reconstruction of copepod co-evolutionary relationships mapped onto it (thin lines). Co-speciation (circles), intra-host speciation (squares) and host switching (arrows) are shown for (a) Gadiformes, (b) Ophidiiformes, (c) Pleuronectiformes, (d) Scorpaeniformes, (e) Zeiformes and (f) representatives from the various fish orders.

not an explanation given the low prevalence and high aggregation of parasitic copepods (Rohde et al., 1995).

One of the features of the TreeMap analyses was the relative lack of sorting events found. This implies that copepod species, once founding successfully on a host species, are relatively unlikely to be lost from the fish species. Copepod larvae have a free-swimming period and are thus able to move themselves to a host. Therefore, if there are any potential hosts in an area, they can be exploited by the copepod larvae. The exception appears to be in the Scorpaeniformes. Of the fish orders examined in this study, the Scorpaeniformes have the most species inhabiting reef systems or other spatially structured habitats. We might speculate that such habitats may restrict the movement of larvae and the opportunities for colonising new hosts. The high number of sorting events implied by the representatives analysis is partially an artefact of a small sample of species taken from a very large taxonomic group (Page et al., 1996).

A surprising result is the relatively high number of intra-host speciation events relative to co-speciation. For example, all studies listed in Paterson & Gray (1999) with as many or more host taxa have fewer intra-host speciation events. This might be an artefact of looking only at the generic level in the fish or it might reflect the potential for allopatric speciation of the copepods on their fish host species if it has an extensive geographical range.

The quality of data is always an important factor in phylogenetic studies. An analysis is only as good as the trees that it is based on. While the phylogenies for both the fish and copepods in this study are the best available, they are far from being the final word on the relationships within these groups. It is important to note, however, that any inaccuracy of the trees should serve to *obscure* any co-speciation signal present (there are many more ways of randomly adding a branch which will decrease matching between two trees than there are that will increase matching). The finding of signal in this study thus implies that the copepod and fish phylogenies are largely accurate, that the co-evolution signal is very strong, or both.

In this study we have shown that *Chondracanthus* spp. and their fish hosts have co-evolved together in four of five fish orders examined. There is also some suggestion of similar co-evolution patterns between the fish orders. There is little evidence for rampant host switching and, while there has been only some co-speciation, there has been an overall history of copepods being passed down each host lineage.

Most work in the area of component analysis of co-evolution has concentrated on lice and their hosts (e.g. Hafner & Nadler, 1990; Page, 1994; Paterson & Gray, 1997), which are host- parasite relationships where close co-evolution is expected. The finding of considerable descent of copepod lineages in conjunction with their teleost hosts is of interest. First, it shows that parasites with free-living stages are not automatically rampant host switchers. Second, it provides support for Fahrenholz's Rule (Brooks & McLennan, 1991) that the null hypothesis of parasite evolutionary descent mirrors host descent. That is, after factoring in the subtle interplay of intra-host speciation, sorting, co-speciation and host switching events, host and parasite trees will be congruent. Finally, it suggests that a closer scrutiny of the co-evolution of fish and their parasites may provide some interesting and novel results.

Acknowledgement

This work is partly supported by a Lincoln University New Developments Grant to AMP.

References

Brooks, D. R. & McLennan, D. A. (1991) *Phylogeny, ecology and behavior: a research program in comparative biology*. Chicago: University of Chicago Press, 434 pp.

Deets, G. B. (1994). Copepod-chondrichthyan coevolution: a cladistic consideration. PhD thesis, Department of Zoology, University of British Columbia, 448 pp.

Deets, G. B. & Ho, J.-S. (1988) Phylogenetic analysis of the Eudactylinidae (Crustacea: Copepoda: Siphonostomatoida), with descriptions of two new genera. *Proceedings of the Biological Society of Washington*, **101**, 317–339.

Dojiri, M. & Deets, G. B (1988) *Norkus cladocephalus*, new genus, new species (Siphonostomatoida: Sphyriidae), a copepod parasitic on an elasmobranch from southern California waters, with a phylogenetic analysis of the Sphyriidae. *Journal of Crustacean Biology*, **8**, 679–687.

Hafner, M. S. & Nadler, S. A. (1990) Co-speciation in host-parasite assemblages: comparative analysis of rates of evolution and timing of cospeciation events. *Systematic Zoology*, **39**, 192–204.

Ho, J.-S. (1991) Redescription of *Chondracanthus zei* Delaroche (Copepoda, Poecilostomatoida) parasitic on *Zeus faber* L. in the Sea of Japan, with a preliminary review of the genus. *Report of the Sado Marine Biology Station* (Niigata University), **21**, 49–79.

Humes, A. G. (1994) How many copepods? *Hydrobiologia*, **292/293**, 1–7.

Kabata, Z. (1981) Copepoda (Crustacea) parasitic on fishes: problems and perspectives. *Advances in Parasitology*, **19**, 1–71.

Nelson, J. S. (1994) *Fishes of the world*. (Third edition). New York: Wiley, 600 pp.

Noble, E. R. , Noble G. A., Schad G. A., & MacInnes A. J. (1989) *Parasitology: the biology of animal parasites.* (6th edition) Philadelphia: Lea & Febiger, 574 pp.

Page, R. D. M. (1990) Component analysis: a valiant failure? *Cladistics*, **6**, 119–136.

Page, R. D. M. (1994) Maps between trees and cladistic analysis of historical associations among genes, organisms, and areas. *Systematic Biology*, **43**, 58–77.

Page, R. D. M., Paterson, A. M. & Clayton, D. H. (1996) Lice and cospeciation: a response to Barker. *International Journal for Parasitology*, **26**, 213–218.

Paterson, A. M. & Gray, R. D. (1997) Host-parasite cospeciation, host switching and missing the boat. *In*: Clayton, D. H. & Moore, J. (Eds). *Host-parasite evolution: general principles and avian models*. Oxford: Oxford University Press, pp. 236–250.

Paterson, A. M. & Gray, R. D. (1999) How frequently do avian lice miss the boat? Implications for coevolutionary studies. *Systematic Biology*, in press.

Poulin, R. (1992) Determinants of host-specificity in parasites of freshwater fishes. *International Journal for Parasitology*, **22**, 753–758.

Rhode, K. Hayward, C. & Heap, M. (1995) Aspects of the ecology of metazoan ectoparasites of marine fishes. *International Journal for Parasitology*, **25**, 945–970.