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Taxonomy of monogenean parasites
and their coevolution with
Australian atheriniform fishes

Thesis submitted by David Brian CORLIS BSc (Hons) UNE

in March 2004

for the degree of Doctor of Philosophy
in Zoology and Tropical Ecology
within the School of Tropical Biology
James Cook University, Townsville

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Taxonomy of monogenean parasites and their coevolution with Australian atheriniform fishes

ABSTRACT

Does a phylogenetic association exist between Australian freshwater fishes and their monogenean parasites and if so what is the nature of the association? Are the associations an example of coevolution, phylogenetic tracking or some other phenomenon? In this thesis I explore these questions.

Knowledge of monogeneans from Australian freshwater fishes is very sparse. To date 26 species of monogenean have been described from 16 species of native freshwater fishes (roughly 5% of the approximately 300 species of freshwater fish known). In the current study I examine a further 19 species of fish from Australian freshwaters.

Studies on phyletic associations can be confounded by taxonomic problems. This is an under-acknowledged problem. Taxonomic understanding of the host group, if vertebrates, is generally better than that of the parasite group. This is certainly true of the atheriniform fish studied here. Here, detailed taxonomic work on previously undescribed parasites is presented. This is based on both morphological and morphometric analysis of dimensions. I erect four new genera of Monogenea in the Dactylogyridae: *Longidigitis* gen. nov., *Recurvatus* gen. nov., *Iliocirrus* gen. nov.and *Helicirrus* gen. nov.and describe 19 new species. The genera are defined by

morphology of the copulatory apparatus while species are defined by haptoral sclerite morphology.

Studies on phyletic associations (coevolution, phylogenetic tracking and cospeciation) typically use comparisons of the phylogeny of the hosts with an independently derived phylogeny of the parasites. Where a single parasite species inhabits a single host species (i.e. is mono-host-specific), comparisons of phylogenies will provide information on the extent of phyletic association, extinction of parasites etc. It is often the case that a single species of parasite inhabits more than one species of host. This can complicate interpretation of the results, but provides an opportunity to discuss phenomena such as host addition, host-switching, rates of cospeciation etc. In the absence of a molecular or morphological-based phylogeny of the parasites, I used data from morphometric analyses to infer a phylogeny.

In this study I recognised that the assumption of mono-host specificity (parasite occurs only on a single host species) is inappropriate as a model for examining coevolution. A much lower level of mono-host-specificity, than previously documented or assumed, was detected which creates many problems for comparing host and parasite phylogenies. Consequently, I developed an approach using the distribution of parasite species among hosts.

A strict one-host one-parasite cospeciation scenario is clearly not apparent for all host species; however a high congruence with host clades is seen in inter and intra specific morphometric variation of parasite and for their associated distribution patterns among hosts. This congruence may be explained by delayed speciation of parasites, since the alternative, extensive host addition, should produce a high level of incongruence with the host phylogeny especially for morphometric variation-derived phylogenies. Whether the patterns of congruence shown represent coevolution or phylogenetic tracking is uncertain. There is clearly a response induced by the host on the parasite in the form of morphometric variation of sclerite variables. Coevolution may be occurring but the high prevalence of parasite infection appears to reject the idea of a parasite-induced host immune response. Thus phylogenetic tracking seems to be the process controlling parasite speciation.

Clustering patterns produced by both methods mentioned above imply a rather high level of congruence with the host clades. These two methods, however, require a well-planned sampling regimen to enable collection of sufficient parasites from sufficient host species and sample sites for pattens to become apparent. It was noted that small sample sets from multiple sites would indicate levels of host specificity better than a large sample set from a single site since, in this study, parasite community structures within sample sites show a high level of prevalence.

Apparent cospeciation between Australian atheriniform fishes and their monogenean parasites is more common in older lineages than in more recently evolved lineages. Two major parasite speciation events were identified, one co-occurred with the speciation event that produced *Melanotaenia trifasciata* and the second with the speciation event that produced the "*nigrans*" clade. Delayed cospeciation is also evident and is reflected in the distributions of parasite species and the inferred parasite phylogenies that used intraspecific variation. If the parasites have not evolved at the same rate, but appear to be one taxonomic level behind the host, then host clades can be identified by the

presence of a particular parasite species. Host addition or switching does not appear to be significant in the monogeneans studied here although possible examples are discussed. Morphometric variation of parasite haptor can be used in phylogenetic studies. Parasite distributions among host species can reflect host phylogeny. Parasite inter-specific associations are strong especially among low host-specific species. Host body length does not appear to affect these interactions. It is clear that when examining phyletic associations of Australian teleosts and their parasites, the host family should be studied as a basic unit.

A phyletic association is present between hosts and parasites and evidence suggests phylogenetic tracking is the process. Cospeciation is common in older host lineages while delayed cospeciation is common in more recently derived lineages.

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DEFINITIONS

Coevolution is the evolutionary association between a host and a parasite, where the population genetic interactions are such that a genetic change in one is followed by a reciprocal change in the other for survival. Coevolution should strictly be used to describe the evolutionary arms race scenario (Blair *et al.*, 2001).

Component Community refers to all infrapopulations of parasites associated with some subset of a host species (Bush *et al.*, 1997).

Component population A parasite component population refers to all the individuals of a specified life history phase at a particular place and time (Bush *et al.*, 1997).

Cospeciation may or may not have a host/parasite interaction causal mechanism. This term has usually been used as a synonym for coevolution and often incorrectly. Coevolution and phylogenetic tracking require cospeciation while cospeciation does not require coevolution.

Delayed cospeciation requires that parasite speciation events occur sometime after relevent host speciation events or visa versa.

Host addition is the establishment of a parasite lineage in a previously unexploited host lineage while still maintaining an association with its previous host lineage (Blair *et al.*, 2001). It may induce parasite speciation through geographical isolation.

Host specificity is defined as the number of known host species on or in which a parasite species may occur (Poulin, 1998). Most studies use data based on the number of host species from which the parasite has been recorded. A more adequate measure of host specificity should take into account the frequency of infection in different species of host and the number of parasites found in each (Rohde, 1993).

Host-switching is the establishment of a parasite lineage in a previously unexploited host lineage, which then evolves with it, abandoning the original host lineage completely or leaving a sister parasite lineage within it (Blair *et al.*, 2001).

Infrapopulation A parasite infrapopulation includes all individuals of a single parasite species in an individual host at a particular time (Bush *et al.*, 1997).

Infracommunity is the assemblage of all individuals of all parasite species within a single host (Bush *et al.*, 1997).

Maximum intensity is the maximum number of individuals of a particular parasite species on a single infected host specimen (Bush *et al.*, 1997).

Mean intensity is the total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of host individuals of that species infected with the particular parasite species. (i.e. includes only infected hosts) (Bush *et al.*, 1997). **Note:** intensity has often been confused with abundance.

Mean abundance is the total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of host individuals of that species examined. This includes both infected and uninfected hosts (Bush *et al.*, 1997). **Note:** intensity has often been confused with abundance.

Metapopulation is defined as all individuals of one parasite species in one population of one host species (Simberloff & Moore, 1997). This definition is applicable to monogeneans since it may be appropriate for monospecific parasites with a direct life cycle (Kennedy, 2001).

Overall prevalence is the number of hosts infected with one or more individuals of a monogenean parasite divided by the number of hosts examined.

Overall mean abundance is the total number of monogenean parasites divided by the total number of hosts examined. This includes both infected and uninfected hosts.

Prevalence is the number of hosts infected with one or more individuals of a particular parasite species divided by the number of hosts examined (Bush *et al.*, 1997). This is expressed as a percentage.

Phyletic association is where a degree of congruence is observed between the phylogenies of hosts and parasites without an identified or implied host/parasite associated interaction being present.

Phylogenetic association is where a degree of congruence is observed between the phylogenies of hosts and parasites and a host/parasite interaction mechanism is identified or inferred. This mechanism can be coevolution or phylogenetic tracking.

Phylogenetic tracking is the association between a parasite and a host, where the host elicits a genetic change in the parasite but the reciprocal is not present. Phylogenetic tracking can still produce congruence between host and parasite phylogenies (Blair *et al.*, 2001).

Synchronous cospeciation requires only that parasite speciation events occur sometime between consecutive host speciation events or visa versa.

ABREVIATIONS

DA1-6. Dorsal anchor measurements.

VA1-6. Ventral anchor measurements.

H1-7. Hook measurements.

VB1-2. Ventral bar measurements.

DB1-3. Dorsal bar measurements.

DFA. Discriminant Function Analysis

PCA. Principle Component Analysis

HCA. Hierarchical Cluster Analysis

LRA. Linear Regression Analysis

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A 3. **RECURVATUS SIGNIFERI** sp. nov. 240

A 4. **HELICIRRUS** gen. nov. 241

A 5. **HELICIRRUS SPLENDIDAE** sp. nov. 243

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