

# Revealing the faunal tapestry: co-evolution and historical biogeography of hosts and parasites in marine systems

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## SUMMARY

Parasites are integral components of marine ecosystems, a general observation accepted by parasitologists, but often considered of trifling significance to the broader community of zoologists. Parasites, however, represent elegant tools to explore the origins, distribution and maintenance of biodiversity. Among these diverse assemblages, host and geographic ranges described by various helminths are structured and historically constrained by genealogical and ecological associations that can be revealed and evaluated using phylogenetic methodologies within the context of frameworks and hypotheses for co-evolution and historical biogeography. Despite over 200 years of sporadic investigations of helminth systematics, knowledge of parasite faunal diversity in chondrichthyan and osteichthyan fishes, seabirds and marine mammals remains to be distilled into a coherent and comprehensive picture that can be assessed using phylogenetic approaches. Phylogenetic studies among complex host–parasite assemblages that encompass varying temporal and geographic scales are the critical context for elucidating biodiversity and faunal structure, and for identifying historical and contemporary determinants of ecological organization and biogeographic patterns across the marine biosphere. Insights from phylogenetic inference indicate (1) the great age of marine parasite faunas; (2) a significant role for colonization in diversification across a taxonomic continuum at deep and relatively recent temporal scales; and (3) a primary role for allopatric speciation. Integration of ecological and phylogenetic knowledge from the study of parasites is synergistic, contributing substantial insights into the history and maintenance of marine systems.

**Key words:** Marine parasites, co-evolution, historical biogeography, marine biodiversity.

*This may be wrong and I would be glad to have anyone disprove the theory as what we want is knowledge, not the pride of proving something to be true.*

Ernest Hemingway (1934) *Out in the Stream: A Cuban Letter; Esquire*.

## INTRODUCTION

Parasite faunas characteristic of marine vertebrates have been assembled through an intricate interaction of history, ecology and geography, as the determinants of organismal evolution and distribution. Elucidation of pattern and process in the origin and maintenance of biodiversity in marine systems follows from studies that integrate phylogenetic approaches and an historical context for biogeography and ecology (e.g. Brooks & McLennan, 1991, 1993*a,b*; Hoberg, 1996, 1997; Page & Charleston, 1998; Brooks & Hoberg, 2000).

Substantial knowledge about species diversity and both host and geographic distribution for a phylogenetically and ecologically diverse array of parasites among fishes, seabirds and marine mammals has been assembled over the past 200 years. Despite a rich base of fundamental knowledge, the parasite

faunas of marine vertebrates have received uneven attention with respect to their co-evolution (encompassing co-speciation and co-adaptation) and historical biogeography within a current methodological framework (Table 1). Thus, although we continue to acquire new information about the distribution of species and higher taxa, we also continue to be challenged to define and understand broad patterns in geographic distribution, host-association and evolutionary history. It is necessary to build a database of comparable studies across an array of taxonomic and geographic scales.

Early studies on faunal distribution and evolution relied on inspection and intuition to define the evolutionary and biogeographic histories for complex host–parasite assemblages; e.g. among marine mammals (Deliamure, 1955) and marine teleosts (Manter, 1966; Lebedev, 1969; and reviewed in detail by Rohde, 1993). These and other monographic studies such as the comparative work on the deep-sea faunas by Campbell (1983) were the precursors or empirical foundations for identifying large-scale patterns in distribution (e.g. depth and latitudinal gradients as outlined by Rohde, 1992, 1993), biogeography or host associations. Often research focused on attempts to use parasites to reveal host evolutionary relationships, or centres of origin and were based on concepts for ‘parasitological

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Table 1. Studies emphasizing an explicit phylogenetic foundation for examination of hypotheses for co-evolution and historical biogeography among marine host–parasite assemblages; including studies of conceptual importance

Date	Author(s)	Area(s)	Host(s)	Parasite(s)	Contribution*
1979	Brooks	General	General	General	Principles, methods, correlation with micro-evolutionary approaches such as Island Biogeography.
1980	Brooks	General	Rockfish	Digenea	Role of phylogeny in interpreting the co-evolutionary relationships between hosts and 'communities' of parasites.
1980 1981	Holmes & Price Brooks	General General	Rockfish General	Digenea General	Rebuttal to Brooks Foundations for Brooks Parsimony Analysis
1981 <sup>b</sup>	Brooks <i>et al.</i>	South America	Chondrichthyes, Potamotrygonidae	Helminths	Empirical tests of origin of freshwater stingrays based on phylogeny, distribution and co-evolutionary relationship of parasites; vicariance vs dispersal; history for marine and freshwater taxa.
1983	Cressey <i>et al.</i>	General	Teleostei, Scombridae	Copepoda	Co-evolutionary relationships; host specificity, biogeography.
1985	Collette & Russo	Pacific/Atlantic	Teleostei, Scombridae	Copepoda	Phylogenies of Spanish mackerels and their copepod parasites; empirical test of co-evolutionary and biogeographic relationships across Panamanian Isthmus.
1985	Brooks	General	General	General	Concept for historical ecology as a research programme.
1986	Hoberg	Holarctic, Beringia	Aves, Alcidae	Eucestoda, Cyclophyllidea, <i>Alcataenia</i> spp.	Co-speciation and historical biogeography of North Pacific basin in Pliocene/Pleistocene; role of colonization in parasite diversification; vicariance and climate; host-specificity decoupled from co-speciation.
1987	Deets	General	Chondrichthyes	Copepoda, Siphonostomatoidea	Parasite taxonomy and phylogeny with discussion on congruence between host and parasite evolution.
1987 <sup>a</sup>	Bandoni & Brooks	General	Holocephala	Gyrocotylidea	Phylogeny of Gyrocotylidea. Co-evolution history attributed to combination of co-speciation and colonization. Indicates origin of gyrocotylids (and host association) predated separation of continents.
1987 <sup>b</sup>	Bandoni & Brooks	Southern Continents	Teleostei	Amphilinidea	Phylogeny of amphilinids. Co-evolution attributed to high degree of co-speciation. Pattern of geographic distribution consistent with vicariance.
1988	Benz & Deets	General	Chondrichthyes; Teleostei, Mobulidae	Copepoda, Cercopidae	Phylogenetic and biogeographic relationships for copepods on epipelagic fishes.
1988	Brooks & Deardorf	Cosmopolitan	Chondrichthyes, Dasyatididae	Eucestoda, Tetraphyllidea; Nematoda, <i>Echinocephalus</i>	Phylogenetic and biogeographic analyses indicate an ancient Tethys Sea-Circum-Pacific origin; supports hypothesis of Pacific origin of Potamotrygonidae.
1988	Brooks & Bandoni	General	Holocephala; Teleostei	Gyrocotylidea/Amphilinidea	Distinguish relictual (i.e., ancient and persistent) co-evolutionary associations from recent colonization matching host phylogeny.
1989	Boeger & Kritsky	General	Chondrichthyes	Monogenea	Co-evolutionary history for Hexabothriidae.
1990 1991	Measures <i>et al.</i> McLennan & Brooks	Australasian General	Chondrichthyes, Rajiformes Teleostei, Gasterosteidae	Monogenea, <i>Monocotyle</i> spp. Helminths	Host specificity. Phylogeny and behavioural characters.
1991	Paggi <i>et al.</i>	Arctic, Atlantic Basin	Pinnipedia, Phocidae	Nematoda, Ascaridoidea, <i>Pseudoterranova</i>	Parasites and sexual selection. Macro-evolutionary tests of micro-evolutionary predictions such as the Hamilton-Zuk hypothesis. Pliocene/Pleistocene history of isolation and diversification, Atlantic sector of Arctic.

1992	Brooks	South America	Chondrichthyes, Potamorygonidae	Helminths	Revisiting of the origin of fw stingrays. Emphasis on the hypothesis that (contrary to previous assumptions of Atlantic in origin), fauna originated from Pacific when Amazon flowed West. First simultaneous reconstruction of host and parasite phylogenies. Marine parasite fauna useful in reconstructing ancient biogeographic relationship between Pacific and Caribbean. Modification of BPA to allow for inclusion of population level data in co-evolutionary studies. Importance of scale in interpreting co-evolutionary hypotheses.
1992	Klassen	General	Teleostei, Ostraciidae	Monogenea	Co-speciation and historical biogeography of Holarctic fauna; colonization and linkage to diversification during Pliocene/Pleistocene. Biogeographic and historical congruence in diversification of phylogenetically disparate avian and pinniped cestodes; Arctic Refugeum Hypothesis; host-switching as driver for diversification in marine systems; models for allopatric speciation.
1992	Hoberg & Adams	Holarctic, Beringia	Pinnipedia, Phocidae, Otariidae	Eucestoda, Tetrabothriidea, <i>Anophryoecephalus</i>	Pliocene/Pleistocene history of isolation and diversification.
1992	Hoberg	Holarctic, Beringia	Pinnipedia, Phocidae, Otariidae; Aves, Alcidae	Eucestoda, Tetrabothriidea, Cyclophyllidea	Use of parasite community structure to differentiate between competing hypotheses for the origin and divergence of American and European eels. Examination of monophyly of host-parasite association; biogeography of Monogenea in tropical oceans. Hypothesis of multiple invasions of parasites, and by implication their hosts, into Caribbean from Pacific. Analytical methods for cospeciation & historical biogeography.
1993	Nascetti <i>et al.</i>	Arctic, Atlantic Basin	Pinnipedia, Phocidae	Nematoda: Ascaridoidea, <i>Contractaacum</i>	Models for allopatric speciation, peripheral isolates; history of Arctic Basin, Beringia.
1993	Marcogliese & Cone	North Atlantic	Teleostei, Anguillidae	Metazoan parasites	Geographic colonization by phocids and subsequent parasite diversification.
1994a	Klassen	General	Teleostei, Ostraciidae	Monogenea	Historical biogeography, co-evolution in marine turtles; complex and deep history for dispersal and vicariance. Host-switching from turtles to marine iguanas.
1994b	Klassen	Atlantic	Teleostei, Ostraciidae	Monogenea	Deep history, putative co-evolution with seabirds subsequent to colonization. Historical biogeography; archaic circum-Pacific distribution.
1994a	Page	General	General	General	Parasites as phylogenetic indicators for hosts.
1994b	Hoberg	Holarctic, Beringia	Pinnipedia, Phocidae	Eucestoda, Tetrabothriidea, <i>Anophryoecephalus</i>	Concepts for historical biogeography and application of host-parasite systems. Comparison of BPA and Component methods for examination of co-evolution. Deep evolutionary history, extending to Paleozoic, involving complex colonization and co-evolution.
1995	Arduino <i>et al.</i>	Antarctica	Pinnipedia, Monachinae	Nematoda, Ascaridoidea, <i>Contractaacum</i>	Bipolar relationships for ascaridoids in phocids; history of isolation and diversification.
1995a	Pérez-Ponce de León & Brooks	Cosmopolitan	Chelonia	Digenea, Pronocephalidae	Allopatric speciation; diversification in Pliocene/Pleistocene.
1995b	Pérez-Ponce de León & Brooks	Cosmopolitan	Chelonia	Digenea, <i>Pyelosomum</i> spp.	Identification of regional centers of diversity for parasites and hosts.
1996	Hoberg	General	Marine birds	Eucestoda, Tetrabothriidea, <i>Tetrabothrius</i>	Re-evaluation of hypotheses for relationships and origins of fresh-water stingrays in Amazonia.
1996	León-Régagnon <i>et al.</i>	Circum-Pacific	Teleostei	Digenea, <i>Opisthadenia</i> spp.	
1996	Thomas <i>et al.</i>	General	Marine fishes	Helminths	
1997	Hoberg	General	General	General	
1997	Hoberg <i>et al.</i>	General	Aves, Alcidae	Eucestoda, Cyclophyllidea <i>Alcataenia</i> spp.	
1997	Boeger & Kritsky	General	Chondrichthyes; Osteichthyes	Monogenea	
1997	Bullini <i>et al.</i>	Antarctica; Arctic	Pinnipedia, Phocidae	Nematoda, Ascaridoidea	
1997	Mattiucci <i>et al.</i>	Boreal; Subantarctic	Cetacea	Nematoda, Ascaridoidea, <i>Anisakis</i>	
1997	Hayward	Indo-West Pacific	Teleostei, Sillaginidae	Monogenea	
1997	Lovejoy	South America	Chondrichthyes, Potamorygonidae	Helminths	

Table 1. (Contd.)

Date	Author(s)	Area(s)	Host(s)	Parasite(s)	Contribution*
1997	Pérez-Ponce de León <i>et al.</i>	Atlantic/Pacific	Teleostei, <i>Albula</i> spp.	Monogenea, Pterinotrematidae	Historical biogeography, co-evolution.
1997	Paterson & Gray	Southern Ocean	Aves, Sphenisciformes, Procellariiformes	Phthiraptera	Co-speciation analysis; methods & protocols for Component/Reconciliation-based studies.
1998	Bray <i>et al.</i>	Tethys Sea	Teleostei, reef fishes	Digenea, <i>Lepidapedoides</i> spp.	Host specificity; broad tropical distribution.
1998	Choudhury & Dick	Atlantic Basin	Osteichthyes, Acipenseridae	Digenea, Deropristiidae	Patterns of co-speciation and vicariance in Cretaceous; relationships of marine and freshwater taxa.
1998	Hoberg <i>et al.</i>	Eastern Pacific	Chondrichthyes, Myliobatiformes	Nematoda, <i>Echinocephalus</i>	Pacific origins for freshwater stingrays of Amazon basin.
1998a	Fernández <i>et al.</i>	General	Cetacea; Pinnipedia	Digenea, Campulidae, Nasitremitidae	Origin of pinniped parasites by colonization from odontocete cetaceans.
1998b	Fernández <i>et al.</i>	General	Cetacea; Pinnipedia	Digenea, Campulidae	Co-evolution and history of campulids and <i>Orthosplanchnus</i> among marine mammals.
1998	Mendoza-Garfias & Pérez-Ponce de León	Atlantic/Pacific	Teleostei, <i>Cynoscion</i> spp.	Monogenea, <i>Cynoscionicola</i>	Historical biogeography, vicariance; Panamanian Isthmus, Pliocene isolation.
1998	León-Régagnon	Pacific	Teleostei	Digenea, Hemiuridae	Historical biogeography and evolution in Pacific and Indo-Pacific reef fishes; host switching & dispersal.
1998	Leon-Régagnon <i>et al.</i>	Tethys Sea, Pacific	Teleostei, Clupeidae	Hemiuridae Bunocotylinea	History of radiation and dispersal in clupeid fishes centered in the Tethys Sea.
1999a	Hoberg <i>et al.</i>	General	Chondrichthyes; Aves; Mammalia	Eucestoda	Deep history extending to Paleozoic for origins of major taxa of marine cestodes.
1999b	Hoberg <i>et al.</i>	General	Aves; Mammalia	Eucestoda, Tetrabothriidea	Origin of tetrabothriids by colonization of basal seabirds in Mesozoic.
1999	Olson <i>et al.</i>	General	Chondrichthyes	Eucestoda, Tetraphyllidea, Lecanicephalidea	Co-evolutionary history, demonstration of host-specific phylogenetic patterns.
1999	Paterson & Poulin	General	Teleostei	Copepoda, <i>Chondracanthus</i> spp.	Co-speciation analyses; deep history of diversification by co-speciation and colonization in a geographically widespread host and parasite assemblage. Testing co-evolutionary models.
1999	Zamparo <i>et al.</i>	Eastern Pacific	Chondrichthyes, Myliobatiformes	Eucestoda, Tetraphyllidea	Pacific origins for Potamotrygonidae in Amazonian freshwater habitats.
2000	Hoberg & Adams	General	Pinnipedia; Cetacea	Helminths	Co-evolution, colonization, temporal and geographic scale, and faunal history.
2000	Brooks <i>et al.</i>	Pacific Ocean	Teleostei, Kyphosidae	Digenea, Lepocreadiidae	Historical biogeography, origins of Pacific taxa; Host switching and geographical dispersal.
2000	Fernández <i>et al.</i>	General	Cetacea, Mysticete	Digenea, Campulidae, <i>Lecithodesmus</i>	Colonization of Mysticete; host-switching processes in diversification.
2000	Nadler <i>et al.</i>	General	Pinnipedia; Aves	Nematoda, Ascaridoidea, <i>Contractaecum</i>	Host-switching among seabirds and pinnipeds.
2000	Paterson <i>et al.</i>	New Zealand, Southern Ocean	Aves, Sphenisciformes, Procellariiformes	Phthiraptera	Co-speciation analyses; comparison BPA & Reconciliation/TreeMap; conceptual issues of co-speciation, intra-host speciation & host switching; deep history of co-speciation.
2000	Rohde & Hayward	Circum-tropical	Teleostei, Scombridae	Copepoda; Monogenea	Structure of tropical faunas; biogeographic barriers to dispersal; Tethys Sea relationships.
2001	Caira & Jensen	General	Chondrichthyes	Eucestoda; Onchobothriidae	Host specificity & coevolution; incongruence for host and parasite phylogenies.
2001	Cribb <i>et al.</i>	General	Fishes, Molluscs	Digenea	Deep evolutionary history, ancestral hosts.
2001	Paterson & Banks	General	General	General	Concepts for co-speciation analyses; comparisons of analytical methods.
2001	Brooks <i>et al.</i>	General	General	General	Current mechanics and applications of Brooks Parsimony Analysis.

\* This category is not meant to be inclusive, merely to highlight specific points relevant to our discussion.

rules' and host specificity (see Rohde, 1993) that have to some extent been superseded (Klassen, 1991; Brooks & McLennan, 1993*a*; Hoberg, Brooks & Siegel-Causey, 1997; Paterson & Banks, 2001). Early empirical observations, however, have often become the focus for recent phylogenetically-based approaches (e.g. Hoberg, 1992; Klassen, 1992; Brooks & McLennan, 1993*a*; Rohde & Hayward, 2000). Still explicit here is the concept, articulated by Manter (1966), that parasites serve as keystones for understanding the history of biotas because of their critical value as phylogenetic, ecological and biogeographic indicators of their host groups (e.g. Brooks, 1985; Brooks & McLennan, 1993*a,b*; Hoberg, 1997; Brooks & Hoberg, 2000).

Parasite faunas of marine vertebrates have been assembled across varying temporal and geographic scales. Further, associations are historically constrained by genealogical and ecological associations (e.g. Brooks & McLennan, 1993*a*). Origins, temporal continuity and structure of marine parasite assemblages can be examined within the framework of hypotheses for co-evolution or colonization that are derived from the comparative study of phylogenies for hosts and parasites generated from analyses based on morphological or molecular data (e.g. Brooks, 1979, 1981; Klassen, 1992; Brooks & McLennan, 1993*a*; Page, 1994*a, b*; Brooks & Hoberg, 2000; Hoberg & Adams, 2000; Paterson & Banks, 2001).

Hoberg & Adams (2000) recently outlined some of the primary criteria for defining associations that have developed through co-evolution versus colonization. Co-evolution, or association by descent, is corroborated through examination and interpretation of host–parasite associations that demonstrate: (1) consistency or congruence in host–parasite phylogenies or area relationships; (2) a high degree of co-speciation or co-adaptation; (3) recognition of phylogenetic or numerical relicts; (4) often widespread geographic distributions, that in marine systems may be global or antitropical in extent. General congruence in biogeographic patterns among complex host–parasite assemblages indicates coincidental physical and biotic processes as determinants of distribution (e.g. Hoberg, 1986, 1992, 1997). In these instances, geographic scale may be linked to the relative age for the initial association of parasite and host taxa, vagility of the assemblage, and duration of their history for co-evolution. Additionally, Hafner & Nadler (1988) and Hafner *et al.* (1994) introduced the concept of temporal comparisons for molecular evolution between hosts and parasites, revealing an important facet to be considered in studies of co-phylogeny.

Faunas derived from a history of colonization contrast with co-evolutionary systems in the following ways: (1) incongruent and inconsistent phylogenies for parasites and hosts; (2) similarities

in host trophic ecology; (3) faunas that are geographically or regionally delimited; (4) parasite faunas in which diversification is temporally circumscribed in the context of the origin and duration of the host group; (5) faunas of low diversity that are depauperate as opposed to relictual; and (6) associations of variable temporal duration and varying degrees of co-speciation/co-adaptation linked to the time frame for colonization of the host clade(s). Page (1994*a*), Paterson *et al.* (2000) and Paterson & Banks (2001) would further suggest that incongruence can arise from events of (1) intra-host speciation (but here incongruence may be a function of scale as demonstrated in an analysis of monogeneans and teleost hosts outlined below), and (2) different patterns of sorting events including extinctions.

Criteria for co-evolutionary or colonizing faunas set a hypothesis-driven framework to evaluate faunal structure in marine systems. Although most current studies on marine helminth systems have applied parsimony mapping (including mapping on both host and parasite phylogenies), or Brooks Parsimony Analysis (BPA) (see Brooks, 1981, 1990; Brooks & McLennan, 1993*a*; Brooks, van Veller & McLennan, 2001; van Veller & Brooks, 2001), alternative analytical methods have been articulated. These include Component or Reconciliation-based approaches which to some degree are now yielding increasingly convergent results with BPA (see Paterson & Banks, 2001). It is not our intent to enter the methodological debate within the context of this paper, but consistently we apply BPA as a primary tool for discovery of underlying patterns and in addressing a range of issues in co-evolutionary and historical biology in marine systems.

The following review explores a range of complex determinants of genealogical and ecological diversity and faunal structure within a phylogenetic framework for host–parasite systems, focusing on helminths, in marine environments. Phylogenetic reconstruction is a powerful and synergistic tool to elucidate the history of marine biotas, and more generally the history of parasites, host–parasite associations and the biosphere (e.g. Brooks & Hoberg, 2000). Using a series of examples from recent phylogeny-based studies (Table 1) we will examine some overlying generalities and contrasting patterns for faunal structure, geographic and temporal scale, and the role of co-evolution and colonization, and articulate concepts for substantial driving mechanisms that influence diversity in marine ecosystems.

#### A DEEP HISTORY FOR MARINE PARASITE FAUNAS

A growing consensus based on phylogenetic studies among higher-level helminth taxa including Digenae, Monogenea, Gyrocotylidea, Amphilinidea and

the Eucestoda across a diversity of host groups encompassing Chondrichthyes, Osteichthyes and the tetrapods clearly indicates a deep age for the origins of parasitic groups among vertebrates (Brooks, 1989; Rohde, 1994; Kearn, 1994; Boeger & Kritsky, 1997; Hoberg, Gardner & Campbell, 1999*a*; Hoberg, Jones & Bray, 1999*b*; Littlewood *et al.* 1999; Cribb, Bray & Littlewood, 2001). Tapeworms appear to have initially diversified among actinopterygian and neopterygian fishes 350–400 million years before present, and chondrichthyans were apparently colonized secondarily (Hoberg *et al.* 1999*a*). Patterns of association for eucestodes appear to parallel those for both Monogenea and Digenea, suggesting that basal diversification for parasitic flatworms coincided with the origins and divergence of lineages for the Chondrichthyes and Osteichthyes prior to the Mesozoic (Brooks, 1989; Boeger & Kritsky, 1997; Cribb *et al.* 2001). This is compatible with a long period of diversification of such eucestode groups as the ‘tetrphyllideans’, Lecanicephalidea, Diphyllidea and Litobothriidae (Hoberg, Mariaux & Brooks, 2001; Olson *et al.* 1999, 2001) among chondrichthyans in marine and secondarily freshwater environments and more generally is indicative of the archaic nature of the faunas in sharks and rays (Euzet, 1959; Brooks, Thorson & Mayes, 1981*b*; Bandoni & Brooks, 1987*a, b*; Brooks & Deardorf, 1988; Brooks & McLennan, 1993*a*; Nasin, Caira & Euzet, 1997). Concepts linked to recognition of a protracted history for tapeworms and various marine host taxa have been articulated by Hoberg *et al.* (1999*a, b*), and emphasize the relictual nature of many groups (see Brooks & Bandoni, 1988). Diversity may have been influenced by radiation subsequent to colonization, or by secondary radiations in contemporary host taxa. A deep history of colonization is apparent, a further indication of the linkage between phylogeny and ecology as factors determining the historical and contemporary structure of parasite faunas in marine environments.

#### *Global extinction and parasite diversity in deep time*

Recognition of deep histories for major parasite taxa has substantial implications with respect to the role of global-level extinction events through Earth history as determinants of faunal structure and geographic distribution (Hoberg *et al.* 1999*a, b*). Pertinent here is the idea that patterns of differential extinction for free-living taxa, across an array of potential intermediate or definitive hosts, have influenced genealogical or ecological diversity for parasites with complex indirect life cycles. Bush & Kennedy (1994) have suggested that extinction at the level of metapopulations would be unlikely but did not discuss this issue in the context of the 7–9 global events now documented for the Phanerozoic (Briggs, 1995).

In the marine environment, extinction horizons may be characterized by ecological perturbations of varying extent and duration leading to rapid elimination or turnover for many taxa (Briggs, 1995; Jin *et al.* 2000). Parasite lineages have persisted in time across a mosaic of ecological stability and disruption, and global-scale extinction events must be viewed as a series of episodic ecological transitions for host-parasite assemblages (e.g. Hoberg *et al.* 1999*a*). Given the scope of past extinction events, e.g. loss of an estimated 90–96% of marine species at the Permian-Triassic boundary 250 MA (Bowring *et al.* 1998; Jin *et al.* 2000), it is probable that the resilience and adaptive plasticity of parasites to respond to rapid environmental perturbation may have been insufficient to lead to temporal and geographic continuity for all lineages and populations (see Bush & Kennedy, 1994). Of particular interest at the P-T boundary is the decimation of late Permian reef communities with complete collapse at the ecosystem level (Briggs, 1995). Among the 7 documented episodes of extinction during the Phanerozoic, there was substantial variation in the diversity of benthic or pelagic taxa involved, regional effects, and the degree to which such environmental crises resulted in major ecological re-organizations (reviewed in Briggs, 1995).

We might ask the following: (1) has differential extinction or turnover of host taxa been an episodic driver of diversification for parasite taxa; and (2) how can we account for taxonomic (or lineage) persistence, and ecological continuity in evolutionary time? It is apparent that parasite lineages where species have complex life cycles dependent on predictable trophic relationships have been persistent; basically lineages have tracked across extinction events. There is a distinction between dependence on a ‘specific’ host, or host taxon, versus dependence on a particular ecological/trophic association, such that it may be transmission dynamics rather than host-association which is conservative in evolutionary time (Hoberg & Adams, 2000).

Lineage persistence and ecological continuity is linked to the interactive effects of differential extinction for intermediate hosts and definitive hosts, or for parasites through the dynamics of host-density effects or stage-specific mortality. Colonization may contribute to continuity through host-switches before, during or after the event horizon; such may involve a switch to an ecologically equivalent group with subsequent radiation (see Hoberg *et al.* 1999*b*). Environmental disruption is predicted to be a driver for relaxation of ecological isolating mechanisms (ecological release) that enhance the potential for host-switching. Alternatively habitat shifts by potential hosts may lead to loss of an assemblage of dependent parasites. Episodic refugial effects and bottlenecks may further lead to punctuated cycles of diversification across a diversity of parasite–host

assemblages, particularly when considered within the context of models for rapid speciation (Hoberg, 1995; Hoberg *et al.* 1999a).

A co-evolutionary component is also involved in lineage persistence. Parasite taxa may persist as (1) relicts of once dominant groups through ancestor-descendant relationships (Bandoni & Brooks, 1987a, b; Brooks & Bandoni, 1988); or (2) as representatives of now extinct host taxa following colonization and co-evolutionary radiation in a novel host group (Hoberg *et al.* 1999a). Recognition of the potential impact of global extinction crises on genealogical and ecological diversity and structure of marine parasite faunas may eventually contribute to explanatory power for understanding patterns of helminth distribution at varying geographic and temporal scales. With refinement of application of molecular clock hypotheses, it may be possible to correlate divergence time for family or ordinal level taxa with particular periods of ecological disruption in Earth history.

#### GEOGRAPHIC AND TEMPORAL SCALE IN MARINE SYSTEMS

One of the questions arising from the issue of the connection between phylogeny and ecology is that of scale and emergent properties. By default, phylogeneticists tend to assume (either implicitly or explicitly) that when a parasite is found on a host it occurs over the entire range of that host. Ecologists have often pointed out the obvious shortcomings of this assumption in criticizing conclusions from phylogenetically-based biogeographic studies. However, with increasingly more detailed distributional data becoming available, it is not always necessary for this assumption to be made. Klassen (1992) has shown that by identifying geographic subpopulations of hosts within their range and identifying parasite distributions within those subpopulations, a data-set can be generated that is analyzable with secondary Brooks Parsimony Analysis (BPA) (see Brooks & McLennan, 1993a; Hoberg *et al.* 1997; Brooks *et al.* 2001), allowing for more refined interpretations of co-speciation and, in particular, colonization events. Klassen demonstrated, for instance, that through this approach, what might have been interpreted as sympatric speciation can actually be seen as allopatric speciation on geographically-isolated subpopulations of the same host species.

A related aspect of scale that has been understudied is seen when enlarging the scope of the analysis; the following example is based on a BPA analysis. That is when a particular group of parasites from a particular group of hosts is studied, one makes (again explicitly or not) the assumption that the basal-most node of the two lineages arose together through co-speciation [a side note is important here: although in

BPA it is not critical nor even necessary to make this assumption, it is typically done; on the other hand Component Analysis or Reconciliation Analysis (e.g. Page, 1994a; Hoberg *et al.* 1997) cannot proceed without this assumption]. Many studies have hinted, *a posteriori*, that this may not be the case. Klassen's work on boxfish parasites indicated clearly two important conclusions about this assumption: (1) later identification of violation of this assumption in no way reduces the validity of the conclusions about the co-evolutionary relationship between the two lineages originally studied. That is to say, this assumption can be made comfortably if the question is specifically about co-evolution between the two lineages (host and parasite) as originally specified. (2) More often than not, one will find that when looking beyond the original two lineages, the assumption invariably becomes weakened. Klassen showed that by expanding the analysis between boxfish and their gill parasites to all teleosts that this group of parasites infect the pattern became both more complicated and more interesting. It became more complicated in that more and more colonization events were uncovered. It became more interesting in that, on a global scale, these colonization events tended to identify ecological association among hosts in specific geographic areas after major and collective vicariant events. This apparently punctuational pattern of co-evolution deserves further investigation.

#### *An empirical analysis of scale*

The most recent and, to some, most promising development toward defining the phylogenetic component of such associations comes with the development of methods for 'controlling for phylogeny' such as phylogenetically independent contrasts (e.g. Harvey & Pagel, 1991). Although this approach has been applied successfully both for free-living taxa and for parasites (e.g. Garland, Harvey & Ives, 1992; Sasal, Morand & Guegan, 1997), controlling for phylogeny is based on the desire to remove the effect of phylogeny (historical constraint) so that the truly interesting ecological questions may be addressed without the confounding effects implicit in differential evolutionary histories. But when the question is one of the interaction between phylogeny and ecology then controlling for, that is removing, the evolutionary variable is not, in our view, the correct approach. Phylogeny and ecology must then, as Brooks has long argued, be examined together. A way must be found to incorporate the one in the other. We present here an example of how this integration may be achieved. The essence of our example involves recognizing the influence that changing the scale of the analysis has on the interpretation of the pattern of association, irrespective of methodology.

Klassen (1992) examined the effect of incre-

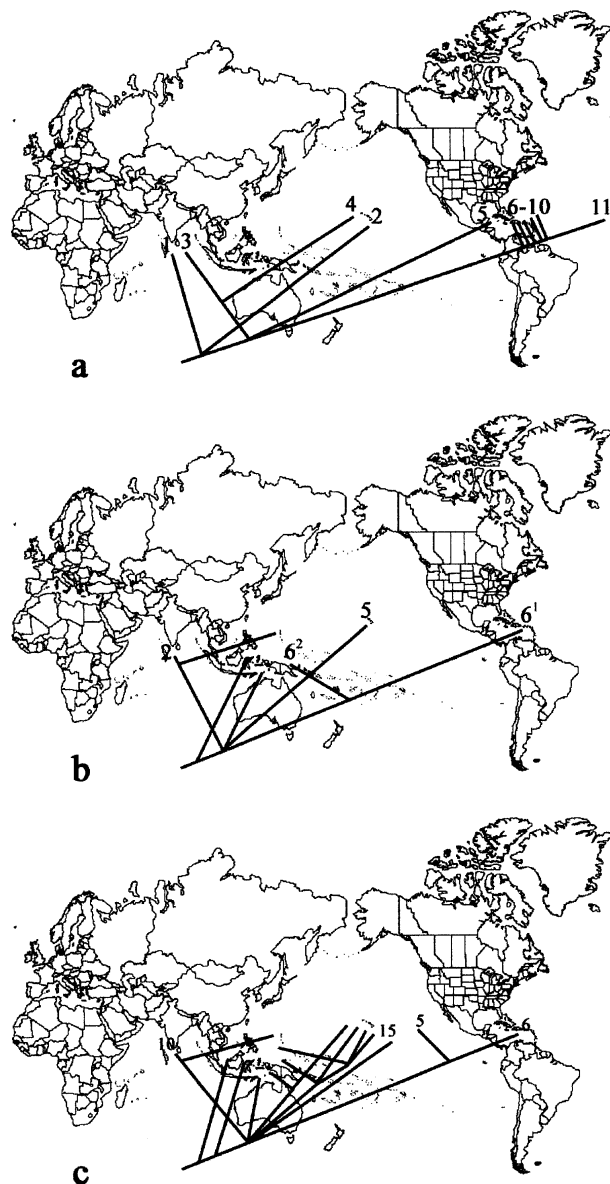


Fig. 1. Reconstruction of area relationship of Ostraciinae boxfishes based on the distribution of their parasites (only host groups including Ostraciidae are labelled). 1a. species-level analysis. 1 – *Ostracion rhinorhynchus*, 2 – *Lactoria* spp., 3 – *Ostracion cubicus* 1, 4 – *Ostracion cubicus*, 2 – *O. meleagris*, *O. cyanurus*, 5 to 11 – Atlantic Ostraciinae in the genera *Acanthostracion* and *Lactophrys*. 1b. family-level analysis, within Tetraodontiformes. 2 – Ostraciidae and triacanthidae, 5 – Ostraciidae and Balistidae, 6<sup>1</sup> – Ostraciidae and Balistidae, 6<sup>2</sup> – Ostraciidae. 1c. 5 – Ostraciidae, Labridae, Mullidae, Balistidae, Chaetodontidae, Ophiidiidae, Apogonidae, Acanthuridae, 6 – Ostraciidae, Labridae, Balistidae, 10 – Triacanthidae, Ostraciidae, 15 – Ostraciidae, Pentapodidae, Balistidae, Chromidae, Pomacentridae, Holocentridae. Modified from Klassen (1992).

mentally expanding the scale of analysis from only boxfish and their parasites, through all Tetraodontiform fishes and their expanded set of parasites to considering the complete suite of Percomorpha hosts of *Haliotrema* parasites. For details of the data and

their analysis the reader is referred to Klassen (1992). Here we will briefly discuss only those aspects that contribute specifically to our changed perception of the co-evolutionary association as scale changes (see Fig. 1). Three specific points can be made about the importance of considering scale. (1) parasite taxa initially identified as species specific (terminal 1 of Fig. 1a) may be shown through subsequent analysis to belong to a parasite clade that parasitizes a larger clade of hosts (terminals 2 and 10 of Figs 1b and 1c, respectively). Thus, the presence of this species-specific parasite on its ostraciine host is the result of speciation through host-switching from an unrelated clade. (2) Scale can be shown to affect the biogeographic component of co-evolutionary interactions. For instance, the species level analysis (Fig. 1a) clearly shows the sister-area relationship between Caribbean and eastern Atlantic (and unresolved relationships within the Caribbean, which we will get back to in the second example) but cannot resolve area relationships between Atlantic and Indo-Pacific. Alternatively, the higher-level analyses (Figs 1b, 1c) cannot resolve within-Atlantic sister-area relationships (due to ‘rounding-error’, see Klassen, 1992) but provide evidence for a Pacific-Atlantic sister-area relationship, not available at the species level. The association, thus, indicates a vicariant event of great age. (3) Further, the association indicates that a whole ecology, not just two lineages, was involved in this event. The Pacific-Atlantic area relationship is supported by parasites from balistids and mullids in addition to ostraciids. The Indo-Pacific area relationship is repeatedly supported by several sister pairs of parasites from a variety of hosts. These repeated biogeographic patterns of co-evolutionary events not only point at various vicariance scenarios not seen in the species-level analysis but also identify groups of hosts likely to be of similar geological age and ecologically associated.

Klassen (1992) also indicated a new approach that would permit exploration of the historical component of host-parasite associations when both host and parasite species are found in, apparently unresolvable, sympatry, specifically the Caribbean clade of boxfish and their parasites. The basic approach is presented here as a 5-step procedure. (1) BPA I analysis. This requires three pieces of information, a host phylogeny, a parasite phylogeny and a host parasite list. The parasite phylogeny and list are then converted to a character matrix for the hosts (see Brooks & McLennan, 1991, 1993a; Brooks *et al.* 2001). This character matrix can then be treated in two ways. The data can be ‘mapped’ onto the host phylogeny. The CI becomes a rough measure of the degree of cospeciation with homoplasy requiring further *a posteriori* explanation (Fig. 2a). Alternately, the data can be used to generate a hypothesis of host relationship on the assumption of strict co-speci-



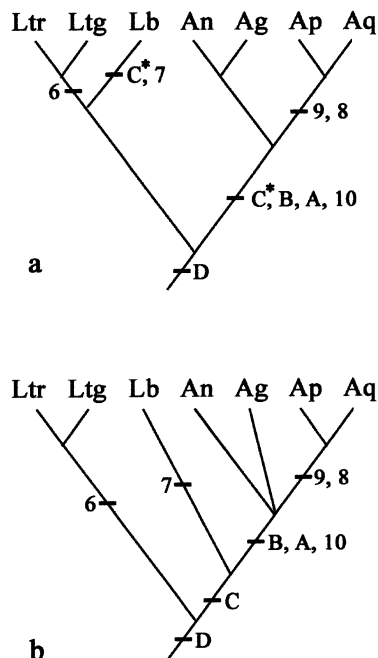


Fig. 2. Results of BPA I analysis for 9 species of *Haliotrema* on 7 species of Atlantic Ostraciinae. Labels at terminal nodes refer to host species. Numbers and letters at internodes refer to parasite taxa mapped as host characters, numbers are the 9 extant taxa, letters represent internodes on the parasite tree. Asterisks refer to events deviating from strict cospeciation, these require further explanation (\* indicates potential host transfer, \*\* indicates sympatric speciation). 2a. Parasite data mapped onto existing host phylogeny. 2b. Parasite data allowed to present their own hypothesis of host relationships. Modified from Klassen (1992).

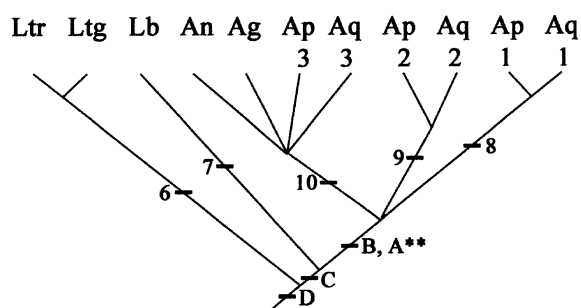


Fig. 3. Results of BPA II analysis for 9 species of *Haliotrema* on 7 species of Atlantic Ostraciinae. Labels as in Figure 2. *Acanthostracion quadricornis* and *A. polygonius* are represented by three terminal nodes each, reflecting the BPA treatment of hosts with multiple parasites (these are treated as separate 'populations' identified by each parasite). Modified from Klassen (1992).

ation. This result can then be compared with the 'true' host phylogeny with consistency indicating co-speciation and deviation requiring further *a posteriori* explanation (Fig. 2b). Typically supporters and detractors alike have focused only on the first of

these options for BPA I. We consistently advocate presenting both as their comparison can help in the first step of resolving the degree to which deviations from the assumption of cospeciation may indicate certain problems.

For instance, Fig. 2 indicates that at least two items require further explanation. In Fig. 2a 'character' C appears to arise twice. If we look at Fig. 2b we see that this case of homoplasy can be resolved if we hypothesize that parasite 7 on host Lb is a case of host transfer (involving speciation). Thus the presence of parasite 7 on its host is due to an ecological association and not co-speciation and the apparent paradox of the parallelism for C disappears. More problematic for BPA I is the presence of multiple parasite 'characters' at two of the hosts internodes. This is seen in both reconstructions (Figs 2a, 2b) and was once interpreted as potential evidence for sympatric speciation.

BPA II was introduced by Brooks (1990) specifically to deal with the coding artifact that seemed to lead to many of these instances of 'sympatric' speciation. Since this artifact is always associated with multiple parasites on a single host, BPA II splits each host taxon with two or more parasites into as many distinct 'populations' as parasites. Fig. 3 is the result of the BPA II reanalysis. Note that this step changes nothing about the presence of parasite 7. It does, however reduce the apparent sympatry to two characters (A and B). This step requires the further hypothesis that the speciation of parasites 8, 9 and 10 occurred not in correspondence with speciation of their hosts but with the isolation of distinct host populations. The apparent sympatry of A and B remains unexplained. So far, this is a typical BPA analysis consistent with currently outlined protocols (Brooks *et al.* 2001).

One of the questions Klassen (1992) asked was whether the hypothetical host populations of BPA II had biogeographic reality. He added a further step to BPA that we will refer to as BPA II-D ('D' for distribution). The subsequent three steps illustrate how the distribution information together with two ecological assumptions may help provide meaningful and predictive hypotheses about each of the associations identified in BPA I as requiring explanation.

Fig. 4 is the BPA II reconstruction with parasite distribution data superimposed. Blanks indicate the absence of a particular parasite from a host for a particular local, 'x' and 'o' indicate presence. The 'o's, however, identify records that are questionable due to low abundances. That is these identify instances when 2 or fewer specimens of a particular parasite were found. Based on the ecological assumption that such rare occurrences indicate 'accidental' infections (an assumption with precedence both in the free-living and parasitic literature, see Esch, Bush & Aho, 1990) any population of host with only an 'o' is removed from the analysis. This results

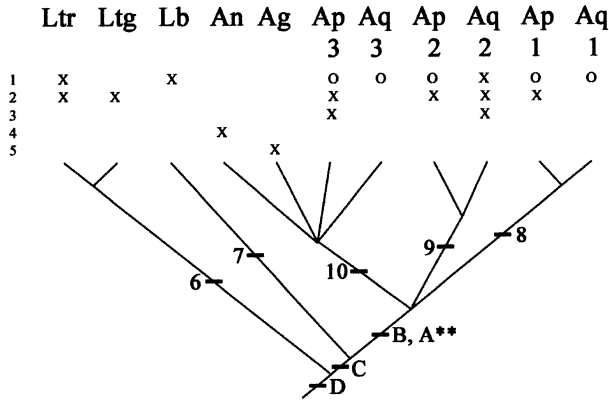


Fig. 4.

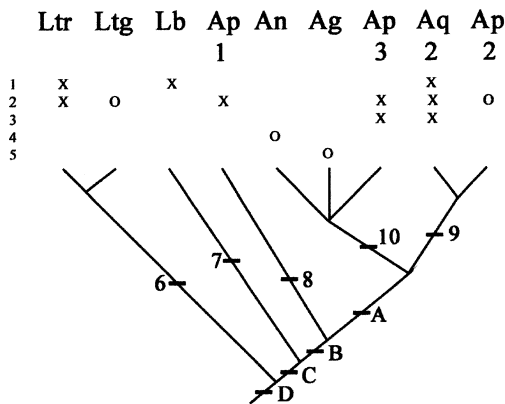


Fig. 5.

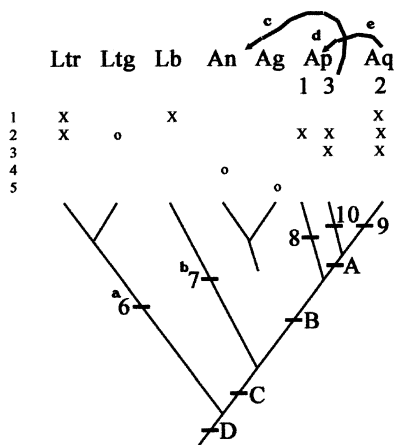


Fig. 6.

Figs 4–6. Results of BPA II-D analysis for 9 species of *Haliotrema* on 7 species of Atlantic Ostraciinae. Labels as in Fig. 2. Additionally, geographic distributions of each parasite for each terminal node are indicated. Areas are: 1 – Coastal North America, 2 – Caribbean, 3 – Coastal South America, 4 – eastern Atlantic (north), 5 – eastern Atlantic (south). X and O refer to relative abundances of parasite on hosts in a particular local. Fig. 4. Same reconstruction as for Fig. 3. ‘x’ indicates confirmed presence, ‘o’ indicates unconfirmed or ‘accidental’ presence (see text for explanation). Fig. 5. Reconstruction after nodes with unconfirmed presences have been removed. ‘x’ indicates ‘core’ host, ‘o’ indicates satellite host (see text for explanation). Fig. 6. Reconstruction after population nodes with satellite presences have been removed. ‘x’ indicates ‘core’ host,

in the reconstruction of Fig. 5. Note now that all putative instances of ‘sympatry’ have been resolved.

A further step involves identifying, for each parasite species, the most likely host (host population) of origin. We have borrowed from Hanski (1982) by distinguishing between core and satellite populations of a species of parasite when found on more than one ‘population’ of host. Thus ‘x’ are core populations by virtue of being more widespread (conversely ‘o’s identify the isolated, stochastic distribution of satellite populations). Further borrowing from the source-sink concept of Island Biogeography (Rosenzweig, 1995) we hypothesize that only core (or source) populations are important in identifying the historical component of the association of these parasites with their host ‘populations’.

The final step in this modified BPA II-D results in a simplified reconstruction of the relationship of host populations based on the combination of parasite phylogenetic and distributional data (Fig. 6). Accordingly, there are a total of five associations between the hosts and their parasites that deviate from the hypothesis of strict co-speciation. They are identified in Fig. 6 with labels a to e. ‘a’ – even though, throughout the unmodified BPA analysis the presence of parasite 6 on its hosts has been considered unproblematic, BPA II-D implies that *Lactophrys triqueter* may be the primary host. ‘b’ – nothing fundamental has changed about the interpretation of parasite 7 on its host. However, taking distribution data into account indicates that the presence of this parasite may be a peripheral isolate. ‘c’ – similar to ‘a’, the presence of parasite 10 on the eastern Atlantic hosts is interpreted as ecological transfer not historical association. ‘d’ – parasite 8 is interpreted as having speciated on a Caribbean population of *Acanthostracion polygonius*. ‘e’ – the presence of parasite 9 on *A. polygonius* is interpreted as dispersal from *A. quadricornis*.

We present this modified approach to BPA as a first step in developing a means of incorporating both phylogeny and ecology in the same analysis. We suggest that the interpretations arising out of such an analysis provide, at worst, a way of developing testable hypotheses that take account of both evolutionary past and ecological present.

General vicariant patterns

Another aspect of scale can be seen in the notion espoused by vicariance biogeographers, that multiple lineage comparisons are necessary for a ‘general vicariant pattern’ to be identified. So far, the empirical data for such a general pattern based on

‘o’ indicates satellite host. Labels ‘a’ to ‘e’ indicate events that require *a posteriori* explanation beyond strict co-speciation (see text for explanation).

parasite lineages among Osteichthyes is lacking. There are, however, indications that these data will soon be forthcoming. First, the study by Klassen (1992) on boxfishes has revealed tentative pattern repetitions when expanding the scale to all hosts of *Haliotrema*; consider the example presented in the previous section. Secondly, two independent studies on Chaetodontidae and Priacanthidae will provide comparative data with those from the Ostraciidae for a quantitative comparison (G. J. Klassen, unpublished data; S. Morand, personal communication).

In contrast, general level or congruent patterns have been demonstrated for phylogenetically disparate groups of tapeworms that infect Phocidae and Otariidae (Pinnipedia) and Alcidae (Charadriiformes) in the North Pacific Basin and across Holarctic seas (Hoberg, 1986, 1992, 1995; Hoberg & Adams, 1992). Similar patterns have also been recognized for ascaridoid nematodes (species of *Contraecum* and *Pseudoterranova*) in phocids and otariids (e.g. Paggi *et al.* 1991; Nascetti *et al.* 1993; Bullini *et al.* 1997, among others). The underlying processes are linked to radiation of hosts and parasites in Subarctic and Arctic refugia during the late Pliocene and Quaternary where refugial effects, habitat fragmentation and isolation were significant determinants of faunal diversification (Hoberg, 1992, 1995; Hoberg & Adams, 2000). Although molecular clock hypotheses have been applied to studies of ascaridoid evolution and biogeography, the temporal setting for diversification among tapeworms, seabirds and pinnipeds has been estimated based on the physical history of the Holarctic region.

The concept for geminate species (Jordan, 1908) is also beginning to receive renewed attention with respect to studies of diversity and relationships of taxa across the Panamanian Isthmus. Although putative species pairs have been recognized and a vicariant history relative to closure of the Panamanian Seaway has been postulated, the phylogenetic context for sister-species has not been firmly established (Marques, Brooks & Monks, 1995; Goshroy & Caira, 2001). Clear patterns have been established for host taxa including marine stingrays, the degree to which the history and distribution of associated species of *Acanthobothrium* and other helminths is congruent remains to be examined (Marques, Centritto & Stewart, 1997).

#### *Archaic taxa and widespread patterns, global and antitropical distributions*

Geographically-widespread parasite faunas encompassing global or antitropical distributions may be indicative of early associations with specific host groups. Although White (1989) has provided for much discussion about antitropical distributions from the perspective of various piscine taxa, and

Briggs (1995) has provided a broader review, parasitological data have yet been applied to this question. One potential source of data would be the parasites of Aracaninae (the sistergroup to Ostraciinae); these fishes have a well understood antitropical distribution, a tropical sister-group and their gill parasites fall into a group that is reasonably well understood (Klassen, 1992). Estimates of divergence time from molecular sequence data for hosts and parasites could further contribute to addressing the relative age and associations for components of widespread faunas.

Among seabirds and marine mammals some parasite groups, including the Tetrabothriidea (species of *Tetrabothrius*) and some Diphyllobothriidae, are geographically widespread, and although some genera are antitropical, species with bipolar distributions have not been identified (Deliamure, 1955; Hoberg 1996). Some evidence suggests that for marine birds, the *Tetrabothrius* faunas characteristic of the Southern Ocean and Northern Hemisphere are distinct and segregated (Hoberg & Ryan, 1987) and that host-specific core faunas may be associated with each of the major orders of seabirds (Hoberg, 1996); monophyly for characteristic species groups remains to be established. Among pinnipeds, the Campulid digeneans are geographically widespread and phylogenetic hypotheses are consistent with a protracted history of colonization and cospeciation (Fernández *et al.* 1998a, b; Hoberg & Adams, 2000).

As a generality, among faunas in marine birds and mammals, and those in chelonians, osteichthyans and chondrichthyans, geographic scale may be linked to age, duration and vagility of the assemblage (e.g. Brooks & McLennan, 1993a; Pérez-Ponce de León & Brooks, 1995a.) Thus, archaic taxa are more often widespread, whereas recent associations may be regional in scale (see Beveridge, 1986; Hoberg & Adams, 2000). A burgeoning body of empirical data from largely descriptive biogeographic inventories provides the foundation for further evaluations of this concept. Rohde (1993) summarized substantial databases for the distribution of digeneans and monogeneans in marine teleosts, providing a comparative context for piscine parasites along latitudinal gradients, and between oceanic regions such as the Pacific and Atlantic basins. A phylogenetic context for such data is critical for understanding the history of faunal assemblage, the interaction of dispersal and vicariance, and the evolutionary relationships of taxa within and among identifiable faunal provinces.

#### *Integration of biodiversity data*

A model for integration of detailed survey and inventory with phylogenetic/historical biogeographic approaches has been exemplified by early and

continuing research on relationships of the parasite fauna of the freshwater rays, Potamotrygonidae, of the Neotropics (e.g. Brooks, Mayes & Thorson, 1981a; Brooks *et al.* 1981b; Brooks & Amato, 1992; Brooks, 1995; Zamparo, Brooks & Barriga, 1999). These studies articulated an hypothesis for Pacific origins of the freshwater stingrays and their parasites. Most recently this theoretical framework has become the focus for ongoing research to reveal the fundamental processes for the history of a major component of the Amazonian biota (e.g. Lovejoy, 1997; Marques, 2000) that can contribute to a more detailed understanding of biogeography and speciation processes during the Tertiary (e.g. Webb, 1995; Räsänen *et al.* 1995). Additionally, regional studies of parasite biodiversity in chondrichthyans from the Gulf of California (e.g. Caira & Burge, 2001; Goshroy & Caira, 2001) are contributing insights to elucidating the broader distribution and history of cestodes in sharks and rays (Caira & Jensen, 2001).

Combined survey and phylogenetic reconstruction are further exemplified by studies of Australian reef fishes (e.g. Cribb, Bray & Barker, 1992; Barker *et al.* 1994; Bray, Cribb & Littlewood, 1998; Bray & Cribb, 2000). Also of note are the detailed biodiversity inventories for coastal waters of Mexico (e.g. Pérez-Ponce de León *et al.* 1999), and their foundation for phylogenetic and biogeographic analyses.

These studies are critical in establishing accurate concepts for host and geographic distribution, and particularly ideas about host-specificity within and among assemblages (e.g. Gibson & Bray, 1994), but need to be considered in an explanatory framework derived from comparative phylogenetics. Although a number of faunal provinces and biotas have received focused attention, there has yet to be a synoptic and integrated approach linking survey, inventory and phylogenetic reconstruction. Such will continue to remain a challenge for any comprehensive work on chondrichthyans, given the exceptional diversity that remains to be discovered and described among the tetraphyllideans and other eucestodes (e.g. Caira & Jensen, 2001). Current methodological development for historical analyses appears to now coincide with increasing knowledge of biodiversity, factors that will promote resolution of history at a broad scale.

Further studies must extend beyond descriptive biogeography which focuses on documentation of distribution, ecological diversity and host association and include integrated approaches to phylogenetic and historical reconstruction (Brooks & Hoberg, 2000). In this manner such questions as how species are related within and between zones and regions or how higher taxonomic groups are distributed in time and space may be addressed. Evaluation of historical structure then becomes the context for identification of common mechanisms involved in distributional history for biotas including the relative roles of

co-speciation or host-switching and vicariance or dispersal. Various facets of history are being increasingly addressed in current assessments of biodiversity and biogeography.

#### CO-EVOLUTION, COLONIZATION AND DIVERSIFICATION

##### *Empirical tests of co-evolutionary scenarios for marine systems*

Although not synoptic for any one host-parasite assemblage or taxon, there are sufficient empirical studies in the literature (e.g. Table 1) to derive a preliminary interpretation of the degree of contribution for co-speciation and dispersal to co-evolutionary scenarios. The majority of these studies have been conducted primarily by inspection and mapping and may benefit from reanalysis according to current comparative protocols, particularly with the potential insights based on inclusion of molecular-based data (see Brooks *et al.* 2001; Paterson & Banks, 2001). Most extensive of these are Brooks' work on stingrays, Collette & Russo (1985) on mackerel, Klassen's on boxfishes, and Hoberg's on the Beringian/North Pacific fauna. Where this has been accomplished, e.g. the studies of *Alcataenia*, the original conclusions have been strongly upheld (see Hoberg *et al.* 1997; Paterson & Banks, 2001). Additionally, Caira & Jensen (2001) reiterated the necessity in co-evolutionary studies to focus on monophyletic taxa and systems with a high level of specificity, accompanied by a robust understanding of host and parasite diversity (accurate taxonomy, identity and comprehensive sampling), and accurate estimates of both host and parasite phylogenies (see also Page, Paterson & Clayton, 1996). We would suggest, however, that the search for pattern and interpretation of process is an exploratory activity rather than an attempt to identify strictly co-evolving systems. Indeed it is discovery of the departures from strict co-speciation (and support for Fahrenholz's Rule) that reveal significant insights into the complex ecological history of faunal associations as indicated for example in the detailed study for *Haliotrema* and boxfishes (Klassen, 1992, 1994a).

The dominant recurring theme evident in diversification of helminth faunas among marine vertebrates including fishes, mammals, chelonians and birds has been colonization. For example, radiation of Trypanorhyncha and the tetraphyllidean assemblage in sharks and rays appears attributable to initial colonization, although a deep history of secondary co-speciation may be indicated by high levels of host-specificity for many species and higher taxa (e.g. Euzet, 1959; Hoberg *et al.* 1999a; Beveridge, Campbell & Palm, 1999; Caira & Jensen, 2001). In general, chondrichthyan faunas have yet to be

examined in great detail based on phylogenetic methods other than through the development of hypotheses for the origins of the freshwater rays, Potamotrygonidae (Brooks *et al.* 1981*b*; Brooks, 1992, 1995), or otherwise in groups of limited scope (Nasin *et al.* 1997; Caira & Jensen, 2001). Host-switching by digeneans and monogeneans has been identified among different groups of teleosts (e.g. Klassen, 1992; Gibson & Bray, 1994; Barker *et al.* 1994; Bray & Cribb, 2000; Brooks, Pérez-Ponce de León & León-Régagnon, 2000). Considerable details, however, remain to be revealed with respect to the co-evolutionary histories of helminth faunas among osteichthyan and chondrichthyan fishes.

The pronoccephalid digeneans characteristic in marine chelonians have also been demonstrated to have a complex history involving extensive colonization, and multiple marine-freshwater transitions (Pérez-Ponce de León & Brooks, 1995*a*). Colonization not only involved habitat shifts for turtles, but shifts by parasites from turtles to such phylogenetically disparate taxa as marine iguanas (Pérez-Ponce de León & Brooks, 1995*b*). The patterns indicated a deep and complex history including vicariance and dispersal.

Among marine homeotherms including cetaceans, pinnipeds and seabirds, few taxa are indicators of historical co-evolutionary linkages, or association by descent, between marine and terrestrial faunas (Deliamure, 1995). Among diphyllbothriids, there is broad evidence for diversification by what has been termed as 'hostal radiation' where ecologically-driven host-switching occurs among phylogenetically-unrelated pinniped or cetacean taxa (Iurakhno, 1991). Phylogenetic studies of the eucestodes have supported an hypothesis for the origin of Tetrabothriidea by host-switching, first to basal marine birds and secondarily to cetaceans and pinnipeds (Hoberg & Adams, 1992, 2000; Hoberg, 1996); co-speciation may have been critical in later diversification of *Tetrabothrius* among avian hosts, but phylogenetic studies have yet to be completed (Hoberg, 1996). Colonization has also been recognized as a significant driver of diversification among the Tetrabothriidea in marine mammals (Hoberg & Adams, 1992) and particularly for *Anophryocephalus* spp. among Phocidae (Hoberg, 1992, 1995). Fernández *et al.* (1998*a, b*) and Hoberg & Adams (2000) demonstrated a complex history involving colonization and co-speciation among odontocetes and pinnipeds for some campulid digeneans. Nadler *et al.* (2000) demonstrated that *Contracaecum* spp. associated with pinnipeds are not monophyletic, and that host-switching among seabirds and pinnipeds has occurred among the ascaridoids.

Additionally, Hoberg (1986, 1992) and Hoberg *et al.* (1997) documented the pervasive nature of colonization in the evolution of *Alcataenia* tapeworms among seabirds of the family Alcidae.

Significantly, the development of marked host-specificity was evident among species that had originated subsequent to relatively recent colonization of host taxa. These studies supported the concept that strict (or 'phylogenetic') specificity should be decoupled from the process of co-speciation, and that the former was not necessarily an unequivocal indicator of the temporal duration of an association (Brooks, 1979, 1985; Hoberg, 1986).

Interestingly, arthropod ectoparasites on both fishes and seabirds may represent a contrast to the histories of colonization being postulated for a variety of helminths and their hosts. The limited number of studies of copepods among teleosts have indicated substantial patterns of co-evolution and co-speciation (summarized in Paterson & Poulin, 1999). Such patterns have been demonstrated among parasite taxa that also exhibit relatively low levels of host-specificity (Poulin, 1992). Further detailed analyses of a wider diversity of copepod taxa and their hosts are necessary to establish this as a generality, but it would provide an interesting comparison to the monogeneans on the same spectrum of piscine hosts (see Rhode & Hayward, 2000).

Phthiraptera among seabirds also appear to have deep co-evolutionary histories with their avian hosts (Paterson, Gray & Wallis, 1993; Paterson & Gray, 1997; Paterson *et al.* 2000). Such may reflect the constraints on the potential for transmission among conspecifics, or for host-switching between phylogenetically unrelated seabirds in relative sympatry at large colony sites (e.g. Paterson *et al.* 2000); the degree of coloniality and the physical attributes of nest sites, and limited interactions during foraging in pelagic situations may serve as substantial controls on distribution. Among the assemblage of lice on both Procellariiformes and Sphenisciformes, co-speciation was postulated as a dominant driver for diversification with contributions from intra-host speciation; patterns of host association were further influenced by sorting events (Paterson, Palma & Gray, 1999; Paterson *et al.* 2000).

Hoberg & Adams (1992, 2000) discussed issues related to host-switching, particularly among marine homeotherms. It is important to note that, among those systems that have been thus far examined based on phylogenetic methods, recognition of widespread co-speciation has not been documented (see also Jackson, 1999). In marine and other systems, host-switching for parasites with complex life cycles is a stochastic process that may be linked to the predictability of guild associations or foodweb structure over extended evolutionary time frames. It is not clear that constraints to host-switching will be the same for parasites with direct versus indirect cycles, or whether ecto- and endo-parasites may be influenced differentially by variation in life history for their respective piscine, avian or mammalian hosts.

### *Vicariance versus colonization*

One of the questions that has often been asked is whether marine systems show similar patterns to those in freshwater and terrestrial environments, or whether patterns in such large and seemingly uniform habitats can even be unraveled. Brooks & McLennan (1993*a*, and references therein) and Hoberg (1986, 1992, 1995, 1997) have addressed this problem theoretically and concluded that there is no particular reason why this should not be the case. Empirically this has now been repeatedly demonstrated; e.g. Brooks *et al.* (1981*b*) and Brooks & Deardorf (1988), Hoberg *et al.* (1998) for parasites of rays, Bandoni & Brooks (1987*a*) for Holocephala, Bandoni & Brooks (1987*b*) as well as Klassen (1992, 1994*a*) for several teleost lineages, and Hoberg (1986, 1992, 1995) and Hoberg & Adams (2000) for seabirds and pinnipeds.

Collette & Russo (1985) seem to indicate, however, that caution must be taken with primarily open ocean pelagic species, the implication being that reconstructing clear patterns may be simplified for taxa in coastal settings. What is missing still is a synoptic work assessing what overall pattern, if any, can be retrieved from these studies collectively about, for instance, the biogeographic relationships between Indo-Pacific, Pacific and Atlantic Oceans. This is particularly important as there appears to be a lack of consensus within the ichthyological community (Briggs, 1995; Palumbi, 1997). Although temporally deep diversification times have been postulated for some parasite–host assemblages (e.g. Rhode & Hayward, 2000 for copepods and monogeneans on Scombridae), molecular divergence studies for such free-living taxa as echinoids and butterfly fishes (*Chaetodon* spp.) suggest active processes for speciation extending through the Pliocene and Pleistocene (Palumbi, 1997).

Rhode & Hayward (2000) examined hypotheses for the efficiency of oceanic barriers to dispersal based on detailed analyses of monogeneans and copepods among scombrid fishes. Centres of diversity for the contemporary fauna were recognized in the Indo-West Pacific and secondarily in the West Atlantic. Closure of the Tethys Sea and associated habitat fragmentation was postulated as a significant driver of isolation and speciation for both monogeneans and copepods on *Scomber* and *Scomberomorus* indicative of a relictual distribution for these assemblages. The East Pacific Barrier was recognized as a major control on the current distribution for these assemblages between the East and West Pacific; such suggests a role as a selective barrier for dispersal for a variety of phylogenetically disparate taxa at differing temporal scales.

A preliminary approach to examination of large patterns in the Pacific was taken by Klassen (1992) who indicated that gill parasites of coral reef teleosts

favoured an Indo-Australian origin for these assemblages; comments on these relationships have been outlined by Marques *et al.* (1997) for species of *Acanthobothrium* in marine stingrays. Further tests of general patterns will be possible in the future as work is currently being conducted independently on the gill parasites of Chaetodontidae and Priacanthidae (G. J. Klassen, unpublished data; S. Morand, personal communication). A combination of these data with that from other coral reef fishes (Klassen, 1992, 1994*a, b*) should permit the derivation of general conclusions about underlying vicariant patterns; an important adjunct to such studies will be inclusion of molecular data in refining ideas about the timing of divergence for populations and species and the physical/environmental determinants of speciation (Palumbi, 1997).

### *Allopatric speciation as a model*

In those systems that have been examined, and particularly among faunas in marine birds and mammals, speciation has been largely allopatric. In these systems, speciation of cestodes and ascaridoid nematodes appears to be driven by the geographic ranges and a history for isolation of definitive hosts (Hoberg, 1995; Bullini *et al.* 1997). Thus, isolation and speciation among diverse assemblages of marine parasites may often proceed independently from that of populations of intermediate hosts. Although different mechanisms for allopatric speciation have been identified (e.g. microallopatry, peripheral isolates) in the speciation of cestodes in pinnipeds and seabirds, all appear to be driven by the particular history of the vertebrate hosts (Hoberg & Adams, 2000). Further for some parasites with direct cycles, the studies of *Haliotrema* outlined above show that many so called scenarios for sympatric speciation may actually represent examples of allopatric speciation for parasites on allopatric host populations. The degree to which allopatry and geographic isolation represent a general model for marine parasites and their hosts remains to be examined in greater detail. In contrast, Rohde (1993) has suggested a role for some form of sympatric speciation to account for the diversity of congeneric species that are encountered in some host individuals. The latter, as indicated above, could be a reflection of our limited understanding of scale in marine systems. Modifications to BPA such as BPA-D as outlined above provide a method for identifying scenarios that might be termed intra-host speciation and a tool for exploring the historical basis for such phenomenon (see also Paterson & Banks, 2001).

### *Intra-host speciation*

Processes for intra-host speciation represent another form or facet of co-evolution (e.g. Paterson & Banks,

2001). They may be invoked based on the observation of the co-occurrence of multiple congeners in single host species, but there are few examples where such systems have been examined phylogenetically. A phylogenetic context is necessary to first demonstrate sister-species relationships and secondarily to discriminate between hypotheses for co-speciation versus forms of colonization. Examples of this phenomenon may be particularly common among genera and species of the Onchobothriidae and Phyllobothriidae in chondrichthyans (Caira, Jensen & Healy 2001) and appear to be commonly reported for species of *Acanthobothrium* and *Pedibothrium* (Caira, 1992; Marques *et al.* 1995, 1997; Caira & Burge, 2001; Caira & Zahner, 2001) and among *Rhinebothroides* spp. (Brooks & Amato, 1992). Paterson & Poulin (1999) identified intra-host speciation as an important process for diversification of copepods of the genus *Chondracanthus* on a variety of marine teleosts.

Assuming that allopatric speciation is a primary determinant for parasite diversification, it may be useful to consider if such intra-host patterns are indicators of punctuated or cyclical/periodic pulses or bouts of geographic isolation for hosts that drive divergence and speciation among parasite lineages (Hoberg, 1995). Duration of isolation may be insufficient to result in divergence for hosts, but may lead to speciation for parasites. Is this a phenomenon linked to the age or geographic extent of an assemblage, in that the influence may be most pronounced among geographically widespread taxa? The issue of geographic and temporal scale is important in this context as it is clear that considerable discrete variation, or species-level partitions that can be demonstrated through comparative molecular analyses are often masked by a similarity or uniformity in morphological characters. Paterson & Poulin (1999) considered that the relatively extensive level of intra-host speciation evident for species of copepods in the genus *Chondracanthus* could reflect allopatric speciation across a broad geographic range occupied by hosts.

Hoberg (1995) suggested that such intra-host patterns were important indicators of cryptic isolation events for components of a host–parasite assemblage. Parasites become cryptic indicators of a complex history of episodic isolation for hosts, and this may either be reflected in the speciose and host-specific nature of some parasite taxa in respective hosts; or may also reflect the facets of biogeographic history that can no longer be recognized for the host group. Of interest would be examination of patterns for episodic isolation linked to marine transgression/regression cycles in the Amazonian basin as drivers of diversification for parasites; speciation may be linked to marine transgression and isolation of discrete drainages over variable time frames since the Miocene (see Webb, 1995; Marques, 2000).

## CONCLUSIONS AND FUTURE DEVELOPMENTS

Phylogenetic studies of parasites and hosts represent a critical context for revealing and understanding patterns in biodiversity, faunal structure and historical and contemporary biogeography (Brooks & McLennan, 1993 *a,b*; Brooks & Hoberg, 2000; Paterson & Poulin, 1999). Phylogeny-based approaches are powerful because hierarchical order constrains the range of explanations for faunal structure and history in a comparative context linking host and parasite taxa. Synergy is evident in integration of phylogenetic, biogeographic, and ecological history in the articulation of synoptic hypotheses for faunal development over often disparate spatial and temporal scales (e.g. Hoberg, 1997). In this regard, parasites constitute exquisite phylogenetic and historical ecological indicators that reveal substantial insights into the history of the marine biosphere. Phylogenetic hypotheses for hosts and parasites are the tapestry for revealing the interaction of co-evolution, colonization and extinction on patterns of faunal structure and ecological continuity across deep temporal and geographic scales in the marine environment.

The great potential for this research programme has been amply demonstrated (Table 1) by an array of studies across a phylogenetically diverse landscape of hosts and parasites (see also Brooks & McLennan, 1993 *a*; Brooks & Hoberg, 2000). Despite nearly 25 years of explicit co-evolutionary studies based on phylogenetic approaches, we still continue to lack critical information for most host and parasite taxa and in many respects the literature is diverse but fragmented. For example, there remains a single detailed historical study of helminths among seabirds (Hoberg, 1986, 1992), and our understanding of species diversity and phylogeny among the speciose tetraphyllidean taxa of chondrichthyan hosts remains to be expanded (Caira & Jensen, 2001). We continue to have relatively few robust species-level phylogenies for parasites within the context of a detailed understanding of relationships for higher inclusive taxa. Likewise, our knowledge of host phylogeny often is inadequate as the basis for modern comparative studies in co-evolution although our basic understanding for relationships among such groups as teleosts (e.g. Stiassny, Parouti & Johnson, 1996), chondrichthyans (reviewed in Caira & Jensen, 2001) and marine mammals (Berta & Sumich, 1999) has dramatically improved in the past decade. Continued expansion of a phylogenetic framework is necessary as a foundation for a detailed and rich comparative research programme; such a situation clearly represents a challenge and an opportunity.

Additionally, Brooks & Hoberg (2000) have emphasized the need to bridge the gap between phylogenetics and ecology, although little effort has so far been put into developing research programmes

that are explicitly directed toward that goal (Brooks & McLennan, 1991). As yet there remains minimal overlap between parasite groups or assemblages for which we have extensive knowledge of community ecology and those which have been evaluated in a phylogenetic context (Poulin, 1998). Brooks (1980) attempted this in the early 1980s to great criticism. McLennan & Brooks (1991) accomplished this successfully in the context of behavioural ecology. Marcogliesie & Cone (e.g. 1993) have been directing their research increasingly in that direction. Klassen (unpublished data) is developing a programme dedicated to both building the empirical data-base needed by both fields and exploring methodological options for integrating micro- and macro-evolutionary approaches.

Burgeoning interest in biodiversity assessment and particularly the Global Taxonomy Initiative clearly indicates a place for parasitological survey and inventory linked to phylogenetic approaches as a cornerstone for future research (Brooks & Hoberg, 2000). Such integrated and comprehensive surveys in marine environments are exemplified in ongoing investigations of the Australian reef faunas, biodiversity survey and inventory in chondrichthyans from the Gulf of California, faunal assessments more widely along Mexican coastal waters, and historical studies of marine-freshwater transitions in Amazonia. We have reviewed an array of interesting examples from a diversity of host-parasite assemblages in marine habitats, but we are challenged to develop broad and synoptic coverage that is necessary to reveal truly general concepts for history across global seas. The time is appropriate for integrative approaches linking systematics, evolutionary biology and ecology in frameworks that can contribute to a more refined understanding of the history and structure of global marine systems and the biosphere.

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