

Evolutionary relationships between trematodes and snails emphasizing schistosomes and paragonimids

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SUMMARY

Snails and digeneans have been associated for at least 200 million years. Their inter-relationships over such a time-span must have been complex and varied. Few studies have attempted to explore these relationships in the light of knowledge of the phylogeny of both host and parasite groups. Here we focus on two important families of digeneans, the Schistosomatidae and the Paragonimidae, for which molecular phylogenies are available. We investigate the types of evolutionary relationships between host and parasite, operating at different phylogenetic depths, that might explain current host specificity and distributions of both associates. Both families of parasites utilise a number of highly diverged gastropod families, indicating that host extensions have featured in their histories. However, schistosomatids and paragonimids show different patterns of association with their snail hosts. As befits the apparently more ancient group, schistosomatids utilise snails from across a wide phylogenetic range within the Gastropoda. The genus *Schistosoma* itself has experienced one long-range host switch between pulmonates and caenogastropods. By contrast, paragonimids are restricted to two superfamilies of caenogastropods. Despite these differences, modern schistosomatid species appear to be more host specific than are paragonimids and host additions, at the level of host family, are far less common among species of schistosomatids than among paragonimids. Some species of *Paragonimus* exhibit remarkably low levels of host specificity, with different populations utilising snails of different families. Existing knowledge relating to the phenomenon will be presented in the context of phylogenies of schistosomatids, paragonimids, and their snail hosts. Discussion focuses on the usefulness of current theories of snail–digenean coevolution for interpreting these findings. In the past, much emphasis has been placed on the idea that digeneans engage in a one-to-one arms race with their snail host. We consider that phylogenetic tracking rather than an arms-race relationship might be a common alternative. Not being bound by the restrictions imposed by an arms race, some digeneans might be able to extend to new host species more easily than the literature suggests. Switches into related host taxa are most likely. However, ecologically equivalent but unrelated gastropod hosts may also be exploited. Given the right ecological setting, digeneans are able to switch across considerable phylogenetic distances. Examples from the Paragonimidae and Schistosomatidae are given.

Key words: Coevolution, DNA sequences, gastropods, historical biogeography, host-parasite relationships, *Paragonimus*, phylogeny, *Schistosoma*.

INTRODUCTION

In recent years, there have been considerable advances in understanding the systematics and phylogenies of both snail and parasite taxa involved in the evolution and deployment of two families of digeneans, the Schistosomatidae and Paragonimidae. These advances permit a critical evaluation of the extent to which these parasites have a shared evolutionary history with their snail hosts and of evolutionary concepts concerning host association and host switching.

Schistosomatids inhabit the blood vessels of birds and mammals, with a single genus and species known from crocodylians. Schistosomatids are found in all temperate and tropical regions of the world,

primarily associated with freshwater habitats. They are atypical digeneans in that they are dioecious and have only two hosts in their life cycles, a gastropod and a vertebrate. There are 13 genera in the family (Basch, 1991). Taxonomy of the type genus, *Schistosoma*, is reasonably settled but the same cannot be said of some other genera. The most recent general texts are by Rollinson & Simpson (1987) and Basch (1991). Paragonimids are lung flukes of mammals (including humans) and utilise fresh or (rarely) brackish water snails and crustaceans as first and second intermediate hosts respectively. The ~ 50 nominal species occur in Asia, Africa and the Americas, mostly in tropical or subtropical areas. More than half of all nominal species occur in East Asia, especially China. A few species are found in temperate regions of North America and Northern Asia. Only two genera are recognized, *Paragonimus* and *Euparagonimus*, but the taxonomy of the family remains confused (see Blair, Xu & Agatsuma (1999) for a discussion of the family).

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A critical examination of molluscan/digenean evolutionary relationships requires knowledge of phylogenies for both hosts and parasites. Few papers have been specifically concerned with comparisons of such relationships. Rather, attention has been paid to phylogenetic analyses of either parasite or snail lineages. Earlier papers on evolutionary associations (Davis, 1980, 1992) focused on the genus *Schistosoma* with special emphasis on Asian species and their snail hosts. Davis, Spolsky & Zhang (1995) and Davis *et al.* (1999) subsequently 'mapped' the historical relationships between species of *Schistosoma* in Asia, and of *Paragonimus* worldwide, on the clades of relevant evolving snail lineages. A later molecular-based phylogenetic analysis of snail lineages transmitting *Paragonimus* in Asia (Wilke *et al.* 2000) resulted in changes in our understanding of some of these lineages and brought into question the long-held assumption of strict molluscan host specificity in tightly coevolved clades of parasites and snails.

Our study relies on accurate identification of snail hosts and parasite species. Most of our host identifications, especially for blood flukes, come from the literature. This is not without its difficulties. Mollusc species are easy to misidentify and the identity of cercariae emerging from a snail may have been proposed because of morphological resemblances to known species. Furthermore, some taxa of digeneans have been based, in part, on the molluscan host in which their cercariae were found. This may lead to excessive taxonomic splitting and can obscure cases of host switching or of continuing uses of multiple hosts.

Molluscan hosts of paragonimids are less well known than those of schistosomatids. Davis *et al.* (1994) made an in-depth annotated review of snail hosts with special emphasis on Asian species and Blair *et al.* (1999) listed known host species. For some species in the present analysis, host identity is inferred from knowledge of the molluscan fauna occurring in the habitats from which infected crustaceans were collected. Consequently, the paragonimid tree contains many question marks against host family names and these host assignments should be regarded as very tentative.

Here we map the molluscan hosts used by schistosomatids and paragonimids onto the most recently available molecular phylogenies of these digenean families, and we map the digeneans on a gastropod phylogeny based on both detailed comparative anatomy and molecular data. The gastropod tree (Fig. 1) is based on anatomical data (Ponder & Lindberg, 1997) with relationships among rissooidean families determined using DNA sequences (Davis *et al.* 1998; Wilke *et al.* 2000). The trees of schistosomatids and paragonimids presented here (Figs 2–4) are compiled from several sources and include some previously unpublished infor-

mation. The data used in each case were sequences of mitochondrial and/or nuclear genes. Approaches to tree construction and interpretation are many and varied. Here we simply present conservative trees, based on the many trees available to us, to provide a summary of relationships. The schistosomatid tree is based largely on Snyder & Loker (2000) with some additional information from Agatsuma (personal communication and Agatsuma *et al.* in press *a, b*). A detailed discussion of the paragonimid taxa sequenced, the trees, their interpretation and the data used in their construction, is in preparation.

Evolutionary terminology

Coevolution is the single term most often applied to describe the evolutionary association between digeneans and gastropods. It was coined by Mode (1958) to describe the genetics of virulence and host resistance among plants and their obligate pathogens. Strictly speaking, the term should not be used except to describe cases where the population genetic interactions of two or more species are such that a genetic change in one elicits a reciprocal genetic change in the other(s). Such mutual evolutionary interactions, in the form of an arms race, have been demonstrated a number of times between digeneans and their snail hosts (see Lively, this supplement), most particularly in cases where a single species of digenean has a high prevalence in the snail population. However, evolutionary interactions between digeneans and molluscs may not always be of this kind, a possibility generally overlooked. Snails possess an internal defence system that lacks immunological memory and seems to be general rather than able to target individual species of digeneans (Wright & Southgate, 1981; Adema & Loker, 1997; Adema, Hertel & Loker, 1999). Consequently, in the typical situation where the prevalence of infection with a single digenean species is extremely low, that particular species is unlikely to have a significant evolutionary impact on the snail. This is not to say that the overall suite of digeneans in a snail population does not elicit an evolutionary response, only that the snail mounts a general response to the different challenges represented by the various digeneans, each with its own evolutionary trajectory. Digeneans utilising the same gastropod species might themselves have conflicts of interest (Poulin, Steeper & Miller, 2000) that could tend to drive snail responses in different directions.

Contrary to the evolutionary indifference that the snail might display towards any single digenean species, the impact of evolutionary or population-genetic changes in the snail must have an enormous impact on each digenean species that utilises it. In other words, the evolutionary fate of the snail may not be influenced by any single digenean species (unless prevalences are atypically high), but that of

the digenean is influenced by the snail. Digeneans must track snails through time but snails need not reciprocate. Use of presumptive terms such as coevolution and its near-synonyms (e.g. co-accommodation and co-adaptation) is inappropriate in such cases. Congruence between host and associate phylogenies can be explained by one of three general scenarios (Brooks & McLennan, 1991): allopatric cospeciation (their 'null' model), phylogenetic tracking and coevolutionary arms race. We consider that coevolution should, strictly, be used to describe only the arms-race scenario. The first two scenarios do not absolutely require *mutual* adaptive responses, a defining condition for coevolution, but may nevertheless lead to congruence of host and associate phylogenies. Strict coevolution is probably best detected at local scales in snail–digenean systems where present-day interactions can be studied in both field and laboratory: its presence cannot be inferred directly from patterns of association.

Other terms to consider are host extension and its components, host-switching and host-addition. Host-switching occurs when a lineage of digeneans establishes itself in, and evolves with, a previously unexploited snail lineage, abandoning the original host lineage completely or leaving a sister parasite lineage within it. Host addition occurs when a digenean adds a new taxon to its existing hosts, most likely in allopatry. Host-switching and host-addition are not mutually exclusive and may operate at different evolutionary scales. The former is more apparent above the taxonomic level of species in digeneans, the latter at the level of species or perhaps species-group. Host addition may be preliminary to host switching. Host extensions are most likely to involve host taxa that are closely related and have a considerable shared genetic heritage. For example, for a parasite normally utilising a pomatiopsid snail, host extension to another pomatiopsid is more likely than to snails of another family. Given the taxonomic uncertainties concerning many hosts and digeneans alike, extensions at shallow phylogenetic levels are likely to be difficult to detect. Consequently, in this paper, we probably over-emphasize the proportion of long-range switches or additions.

We can make a number of predictions about host addition. It involves extending the range of a digenean species by adding new snail hosts, almost certainly in allopatry. We predict that the first individuals of a species that are successful in parasitising a novel snail host produce few cercariae and may face other fitness penalties. Consequently, when novel hosts are added in sympatry with canonical hosts, the alleles permitting the addition are likely to be diluted out and hence selected against. In allopatry, this cannot happen and any parasites persisting in the novel host presumably increase their compatibility with it through time.

Host addition may induce parasite speciation

through geographical isolation (allopatric speciation) and/or founder effects involving the parasite population. Note that allopatric speciation in such a case is not cospeciation (the 'null' model of Brooks & McLennan, 1991): the parasite need not be speciating in response to speciation by a host. The geographical dispersal of parasites that might lead to host addition is presumably mediated by vagile and migratory hosts such as birds. Parasites may thus be maintained in unrelated snail species at different points along a migratory route. Of course, migrating hosts could easily transport, to the same locality, individuals of a parasite species (which may also inhibit parasite speciation) that differ in snail compatibility. This might explain the discovery in the same pond of two forms of the echinostomatid digenean *Echinoparyphium recurvatum*, one infecting a lymnaeid snail and the other a valvatoid (McCarthy, 1990). Similarly, a single nominal species of *Typhlocoelum* (Digenea: Cyclocoelidae) has sympatric forms that each utilise one of three families of pulmonates (Scott, Rau & McClaughlin, 1982). *Echinoparyphium* and *Typhlocoelum* both occur in birds.

We predict that examples of host addition will best be recognized by comparing digeneans from different points along migratory routes, on opposite sides of biogeographic boundaries where snail faunas differ, and between marine and freshwater habitats. It might also be instructive to examine digenean taxa that include among their host taxa, snail families that are apparently permissive hosts, such as pomatiopsids (see below) and possibly also ancyliids (Cable & Peters, 1986). Patterns of host addition by digenean species distributed around the world by human activities might also repay study. To confirm host addition, it will be necessary to show that the parasites occurring in different hosts and locations belong to the same species or species group, a task for which molecular genetic methods are well suited.

MOLLUSCAN PHYLOGENY AND RADIATION

Re-evaluation of molluscan phylogeny over the past several years has radically changed the traditional classifications of the past 60 years. The most important synthesis to date is that of Ponder & Lindberg (1997) providing the basis of the phylogeny presented here (Fig. 1).

There are over 100 000 species of molluscs of which some 60% are gastropods that are distributed among three main lineages (Caenogastropoda, Valvatoidea and Euthyneura, the last two in the Heterobranchia). The 'prosobranch' caenogastropods arose first in the sea and then moved into freshwater and onto land. The early heterobranchs gave rise to the Valvatoidea and Euthyneura in the Carboniferous. The former lineage has retained some prosobranch features whereas the latter is more derived. The

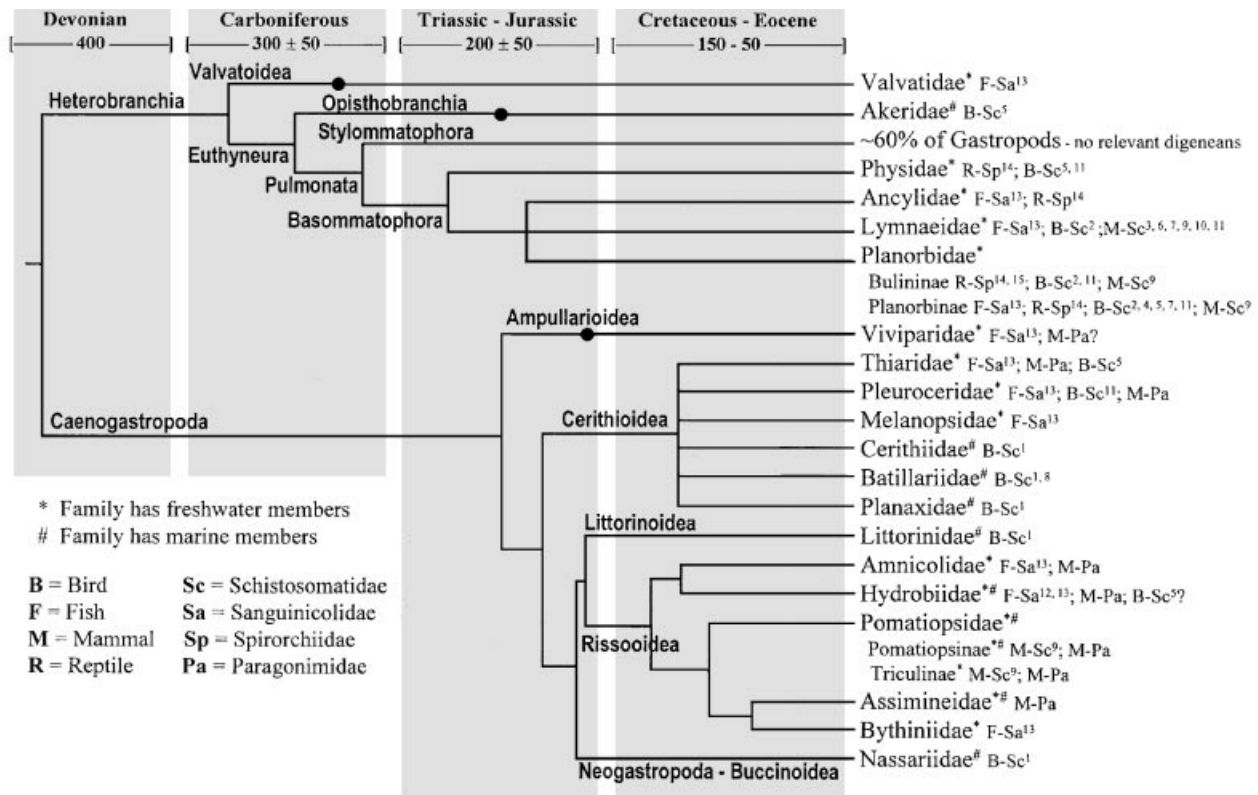


Fig. 1. Phylogeny, classification and approximate ages of the gastropod taxa relevant to this paper. Divergence dates within the Devonian and Carboniferous periods are uncertain, and these parts of the tree should be regarded only as an indication of order of divergence. Closed circles on branches leading to Valvatidae, Akeridae and Viviparidae indicate approximate times at which those families appeared. Note that our understanding of relationships among rissoidae families discussed here is likely to change in the near future (Wilke *et al.* 2000 and Davis, unpublished). In particular, hosts of *Paragonimus* in Central and South America that are usually regarded as members of the family Hydrobiidae should probably be referred to the Cochliopidae. Parasite families and their vertebrate host taxa are shown after each gastropod family name. Superscript numbers denote parasite genera as follows. Schistosomatidae 1, *Austrobilharzia*; 2, *Bilharziella*; 3, *Bivitellobilharzia* (not included in molecular tree); 4, *Dendrobilharzia*; 5, *Gigantobilharzia*; 6, *Heterobilharzia*; 7, *Orientobilharzia*; 8, *Ornithobilharzia*; 9, *Schistosoma*; 10, *Schistosomatium*; 11, *Trichobilharzia*. Sanguinicolidae 12, *Paracardicoloides*; 13, *Sanguinicola*. Spirorchiidae 14, *Spirorchis*; 15, *Enterohaematotrema*. Gastropod families with freshwater members are indicated by * and those with marine members by #.

major euthyneurous lineages are the marine Opisthobranchia (marked by a progressive and rapid loss of the shell) and the Pulmonata that evolved on land and in freshwater (gills replaced by a 'lung' and typically with a shell). The Pulmonata have two orders (or sub-orders). The Basommatophora are freshwater and the Stylommatophora are terrestrial. It is acknowledged that the Opisthobranchia and Pulmonata are paraphyletic or polyphyletic to some degree yet to be determined (Ponder & Lindberg, 1997), but the terms still serve the purpose of pointing out the main evolving clades of concern here.

The divergence of the Caenogastropoda and the Heterobranchia can be traced back to at least the Lower Carboniferous (325 to 360 MYa) (Kollmann & Yochelson, 1976). The heterobranchs were already well diversified by then suggesting an even earlier origin (Ponder & Lindberg, 1997), perhaps in the Devonian as shown in Fig. 1. All the major snail

clades (caenogastropods, valvatoids, opisthobranchs and pulmonates) were present during, and impacted greatly by, the major Permian extinction (286–245 MYa). Consequently, we trace the flowering of the modern gastropod radiations in freshwater and land to the Mesozoic, especially the Jurassic and Cretaceous when sufficient fossil beds were laid down enabling some discernment of the distributions of snail families and their ecologies. The pulmonate Physidae possibly arose in the Carboniferous, but were well established in the fossil record along with the Lymnaeidae and Planorbidae (Bulininae) by the Jurassic (208–146 MYa) (Wenz, 1939). The rissoidae-hydrobioid radiations were well established by the late Triassic and early Jurassic (210–146 MYa) in what are now South Africa and India (Davis, 1979, 1980; Ponder, 1988). The Amnicolidae stem from the Cretaceous (Wenz, 1939). *Littorina* (Caenogastropoda: Littorinoidea) was found in the Triassic (245–208 MYa). The

Valvatoidea are found in the Carboniferous; the Akeridae, the Jurassic and the relevant cerithioideans, in the Cretaceous. Some brackish and freshwater families can only be traced to the early or mid-Tertiary of the Cenozoic Era (65–5 MYa), e.g. the rissooidean Assimineidae and Bithyniidae, but probably had earlier origins.

We can trace with some confidence the biogeographic histories of many of the gastropod families important to our discussion. Davis (1979, 1980) documented the centre of origin of the family Pomatiopsidae in what are now southern Africa and India, with the break-up of Gondwana moving snail families to what are now South America, Australia, India, and presumably Antarctica. The Miocene collision of the Indian Plate with Asia created the Himalayan orogeny, which initiated an ecological revolution by rapidly creating and destroying freshwater environments and accelerating the evolution of the major rivers of eastern Asia with all their attendant stream captures. Pomatiopsids, already differentiated into triculines and pomatiopsines, moved east and south along these evolving river systems. The amphibious *Oncomelania*, the only genus of the subfamily Pomatiopsinae in China and eastern Asia (Japan, Taiwan, Philippines, eastern Indonesia), tracked a relatively uniform ecology and formed a limited morphostatic radiation of two species, one of which, *O. hupensis*, comprises several subspecies. The genus also dispersed to North America where it gave rise to the sister genus *Pomatiopsis* (Davis, 1979, 1980, 1981). The subfamily Triculinae is found only in an arc from northeast India into northern Burma and China-southeast Asia. The rapid ecological changes during the late Miocene–Pliocene left behind a rich fossil record, especially of triculine taxa, in ancient lake beds in northern Burma. Triculines form a wholly aquatic group exhibiting today an amazing adaptive radiation of three tribes, over 20 genera and more than 120 species. Two tribes are remarkable adaptive radiations invading lakes, streams, and every conceivable niche in the Mekong River that experiences dramatic annual fluctuations in flow due to the monsoons.

The same generalised track as followed by the pomatiopsids, from India into northern Burma and China, and hence into southeast Asia, is observed in other relevant snail families, such as the Planorbidae and Thiariidae. The pulmonate family Planorbidae has two prominent subfamilies, the Planorbinae and Bulininae. The latter radiated in Africa as the genus *Bulinus* and in India as *Indoplanorbis* with subsequent introduction and dispersal in southeast Asia. The former subfamily, the Planorbinae, occurs in Africa and South America. The cerithioidean *Brotia* (Thiariidae), transmitting *Paragonimus* in eastern Asia, also occurs in a generalised track from India into southeast Asia (Malaysia to the Philippines).

ORIGINS OF SNAIL–DIGENEAN ASSOCIATIONS

The origins of digeneans and the steps leading to their host commitment to molluscs are unknown but often speculated upon. Gibson (1987) and Gibson & Bray (1994) proposed that proto-trematodes first parasitised molluscs (possibly bivalves) at least 400 MYa, later transferring to gastropods and, in one case, to scaphopods. The association with vertebrates, and hence the appearance of digeneans, probably started about 200 MYa when modern teleosts evolved. By this time the families of gastropod heterobranchs, superfamilies of caenogastropods and all higher taxa were well established. If this view is correct, and the digeneans arose only once from the flatworms associated with the gastropods of the time, then the early radiation of the Digenea must have been accompanied by much host-switching among snail families from the plesiomorphic host. It might also have been the case that host specificity with respect to the gastropod was less marked than at present (Gibson & Bray, 1994), in which case several molluscan taxa could have provided effective alternative hosts for each early digenean group.

PARASITE PHYLOGENIES AND HOST RELATIONSHIPS

The Schistosomatidae

Blood flukes belong to three related families and occur as adults in the blood vessels of fish (Sanguinicolidae), turtles (Spirorchiidae) and crocodilians, birds and mammals (Schistosomatidae). Members of all families occur in both marine and freshwater habitats. A phylogeny of the blood flukes (Fig. 2) provides a molecular-based road map of their evolution and permits a discussion of snail host associations. This discussion should start by trying to infer the ancestral host taxon for the schistosomatids, a task that is far from easy.

As seen in Fig. 2, sanguinicolids and spirorchiids are outgroups for the Schistosomatidae. Blood flukes and the related strigeoids appear to be the earliest diverging digeneans (Cribb *et al.* 2001). Sanguinicolids, associated with fish, may represent the basal diverging lineage within the Digenea. Modern freshwater sanguinicolids use a wide range of snail families in all main lineages (11 families in 6 superfamilies – see Fig. 1). Hosts for the many marine sanguinicolids, excluding the aberrant *Aporocotyle*, are not known. Where known, species of *Aporocotyle* utilise polychaete annelids as the sole intermediate host (Køie, 1982)! Cercariae thought to be those of sanguinicolids have been found in marine bivalves (Smith, 1997). The sanguinicolids therefore provide no clues as to the plesiomorphic molluscan host for blood flukes. Indeed, it is possible that this

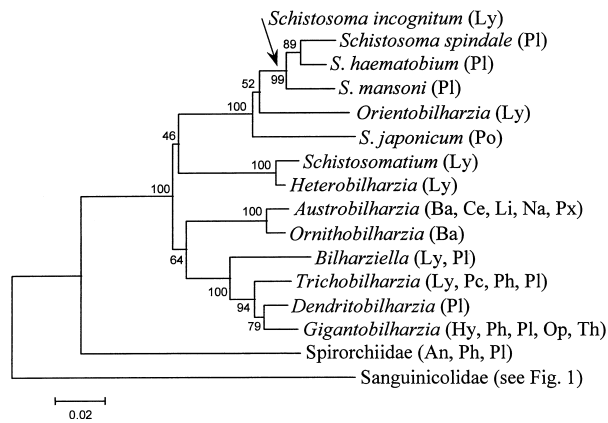


Fig. 2. Distance tree of relationships within the Schistosomatidae. This phylogeny is based on molecular data from the nuclear 28S ribosomal RNA gene and includes 10 of the 13 recognized genera of schistosomes (Rollinson & Southgate, 1987; Basch, 1991). A sequence for *Schistosoma spindale* (GenBank accession number Z46505) was added to the data of Snyder & Loker (2000). Sequences were aligned using ClustalW (Higgins, Thompson & Gibson, 1996). A distance matrix was constructed in MEGA2 (Kumar *et al.* 2000) using the Kimura 2-parameter model (with complete deletion of indels) and trees constructed using the minimum evolution method (1000 cycles of bootstrapping). Bootstrap values are shown in percentages. Molecular data from other gene regions indicate the internode (arrowed) on which *Schistosoma incognitum* should be joined to this tree (Agatsuma, personal communication and in press *b*). The tree is rooted by inclusion of the outgroup families Sanguinicolidae and Spirorchidae. Note that this tree differs somewhat from that published by Snyder & Loker (2000): The clades (*Heterobilharzia* + *Schistosomatium*) and (*Ornithobilharzia* + *Austrobilharzia*) have exchanged places and the root of the Schistosomatidae has been placed so as to include the former clade in a lineage with *Schistosoma* and *Orientobilharzia*. We regard these differences as due to the presence of two very short, adjacent internodes that produce instability in that portion of the tree. Where known, the family or higher taxon of snail hosts is indicated: An, Ancyliidae; Ba, Batillariidae; Ce, Cerithiidae; Hy, Hydrobiidae; Li, Littorinidae; Ly, Lymnaeidae; Na, Nassariidae; Op, Opisthobranchia; Pc, Pleuroceridae; Ph, Physidae; Pl, Planorbidae; Po, Pomatiopsidae; Px, Planaxidae; Th, Thiaridae. For molluscan hosts of sanguinicolids, see Fig. 1 and the text.

family has retained the broad host specificity suggested for early digeneans by Gibson & Bray (1994). Such a breadth of host taxa does not occur in the more derived blood flukes (Spirorchidae and Schistosomatidae). Perhaps by the time these had evolved, the bloodfluke lineage had already settled into tracking one or a few host lineages.

Spirorchids in freshwater habitats utilise pulmonate snails. Hosts for this family in marine habitats, where many species occur, are unknown.

Marine pulmonates could possibly be involved, e.g. the Siphonariidae that are numerous and intertidal, or the Ellobiidae abounding in salt marshes, but data are lacking. Schistosomatids utilise pulmonates, caenogastropods and even opisthobranchs. The one schistosomatid species occurring in a freshwater crocodile (Platt *et al.* 1991) is presumably basal in the family. There is anecdotal evidence that the host for this schistosomatid is a pulmonate (Platt *et al.* 1991). We consider that pulmonates were the ancestral host taxon for schistosomatids, but acknowledge that the evidence is far from conclusive. Pulmonates are included among known host taxa for sanguinicolids and spirorchids. They are also hosts (where known) for all schistosomatid genera except those in the clade *Austrobilharzia* + *Ornithobilharzia*, some species of *Gigantobilharzia*, one of *Trichobilharzia* (*T. corvi*) and for the *Schistosoma japonicum* and *S. sinensium* groups. The case of *Schistosoma* species in non-pulmonates is discussed in detail below and considered to be a consequence of a host-switch during the Tertiary. *Trichobilharzia corvi* belongs to a large, cosmopolitan genus in which all other members occur in pulmonates. The switch to a caenogastropod was presumably recent. In the remaining cases, the non-pulmonate hosts are marine. *Gigantobilharzia huttoni* is the only schistosomatid to utilise an opisthobranch. Again, this is presumably a relatively recent switch: most other members of the genus utilise pulmonates with two reports from caenogastropods. In the case of *Austrobilharzia* + *Ornithobilharzia*, given the rather basal position this clade occupies in the tree (Fig. 2) it is less easy to be certain that the snail hosts have not been retained from a plesiomorphic condition. However, we suspect that *Austrobilharzia* + *Ornithobilharzia* have switched to caenogastropod hosts relatively recently as a consequence of targeting sea birds. Host-switching associated with a change in ecology is discussed later.

We will now turn to the genus *Schistosoma*. Species within *Schistosoma* are usually placed into different groups according to snail host specificity and egg shape (Rollinson & Southgate, 1987). The *S. japonicum* group (defined by Davis & Greer, 1980) occurs in east and southeast Asia and utilises pomatiopsid snails (both Pomatiopsinae and Triculinae). Its members have round eggs with a recessed spine. The southeast Asian *S. sinensium* group has a rather more restricted range centred on southwest China and northern Thailand and occurs in triculine snails. It has elongated asymmetrical eggs with a lateral spine somewhat resembling those of the *S. mansoni* group.

The *S. mansoni* group, consisting of relatively few species, has elongated eggs with a lateral or sub-terminal spine. Two species, *S. mansoni* and *S. rodhaini*, are very closely related to each other (Després *et al.* 1992). The remaining two species

occur in *Hippopotamus* and we are not convinced that they should be grouped with *S. mansoni* despite their egg shapes. Certainly, limited molecular data for one of these, *S. hippopotami*, suggest it lies basal to all African *Schistosoma* species (Després *et al.* 1995). The *S. mansoni* group is centred on Africa with introduction to the Americas (Després, Imbert-Establet & Monnerot, 1993). *Schistosoma mansoni* is associated with *Biomphalaria* of the Planorbidae, subfamily Planorbinae (see various papers in this supplement).

All remaining *Schistosoma* species (*S. haematobium* complex in Africa and the probably paraphyletic '*S. indicum*' group in India and southeast Asia) have elongated eggs of varying morphologies but always with a terminal spine of some sort. Most *Schistosoma* with terminal-spined eggs are associated with the Planorbidae, subfamily Bulininae. In Africa the bulinine snails are *Bulinus* while in India and southeast Asia the relevant genus is *Indoplanorbis*. The exception is *S. incognitum*, a member of the *S. indicum* group that utilises lymnaeids. In molecular trees (e.g. Fig. 2 and Agatsuma *et al.* in press *b*), this species lies basal to all African species (except possibly for *S. hippopotami*) and the remaining members of the *S. indicum* group. The four species of the *S. indicum* group have the same generalised track as *Indoplanorbis* and other snail taxa, from northeast India to Burma and dispersal into southeast Asia.

The genus *Orientobilharzia* (lymnaeid snail hosts) consists of about 4 species occurring in India, parts of southeast Asia, and in a broad band in the temperate zone from Turkey to northeastern China. Surprisingly, Snyder & Loker (2000) found that sequence data for *O. turkestanica* rendered *Schistosoma* paraphyletic in their molecular trees (Fig. 2). It may be that members of this genus should be absorbed into *Schistosoma*, or else that *Schistosoma* itself needs to be split. Certainly, molecular data (Barker & Blair, 1996; Snyder & Loker, 2000; Le *et al.* 2000) and cytogenetic evidence (Hirai *et al.* 2000) indicate marked divergence between the species using pomatiopsid snails and those using pulmonates. Baugh (1977) has suggested that *Orientobilharzia* may not itself be a natural taxon. Clearly, full appreciation of the history of *Schistosoma* requires further work to be done on the genus *Orientobilharzia*.

Interpretations of snail–parasite relationships require an understanding of the timing of events. For the species of *Schistosoma*, views on biogeographic origins and ages fall into two main camps differing on matters of timing: one invokes primarily vicariance, the other dispersal. The former hypothesis places the origin of *Schistosoma* in Gondwana (an area overlapping Gondwanan India, Africa and presumably Antarctica) during the Cretaceous with one or more lineages of the genus

subsequently introduced to Asia on the Indian Plate. The latter hypothesis has the genus originating somewhere in Asia, with a Miocene/Pliocene dispersal to Africa.

The Gondwanan-origin (vicariance) hypothesis was proposed and voluminous documented by Davis (1979, 1980, 1992). According to this, ancestral *Schistosoma* species were associated with pulmonate snails in Gondwana, especially in an area overlapping conjoined eastern Africa and India. As the supercontinent broke up, the ancestors of the Asian *Schistosoma* species rafted there on the Indian plate (which split from Africa at least 75 MYa in the late Cretaceous), leaving behind in Africa the ancestors of the modern African species. The collision between India and Asia during the Miocene caused the Himalayan orogeny and had a profound effect on the evolution of *Schistosoma* in the region. One clade, committed to the pomatiopsid snails which had accompanied them on the Indian plate, evolved down the huge river systems developing to the east and south and gave rise to species of both the *S. japonicum* and *S. sinensium* groups. Members of the *S. indicum* group retained their allegiance to pulmonates and remained in India or dispersed into southeast Asia, following the same pathway of introduction as the pomatiopsid snails.

The strengths of this argument are the congruence of the tectonic history, area cladograms and evolution of the relevant snail lineages. For example, the *S. haematobium* group has formed a considerable radiation in Africa in association with bulinine planorbids of the genus *Bulinus* while other terminal-spined schistosomes radiated in India in *Indoplanorbis* (the only other bulinine genus) with subsequent introduction to southeast Asia. These bulinine taxa are known to be an ancient lineage (fossils date to pre-Cretaceous, Wenz, 1939; Planorbinae and Bulininae in Africa and India in the mid to upper Cretaceous – Newton, 1920). A possible weakness of the argument is that, according to molecular trees (Fig. 2), two lineages (*S. japonicum* + *S. sinensium* and the lineage leading to *Orientobilharzia*) occur only in Asia and the basal member (*S. incognitum*) of the third lineage occurs in Asia today. (Some molecular evidence indicates that one African species, *S. hippopotami*, lies at the base of the clade including the African species (Després *et al.* 1995) and members of the *S. indicum* group (Agatsuma *et al.* in press *b*), but further data are required to confirm this.) If Gondwana is the ancestral home of the genus, then the three main clades must have existed before the break-up of Gondwana and two of them subsequently became extinct in Africa or were never in the African part of Gondwana. This also implies an origin for the genus in the mid-Cretaceous, followed by little morphological diversification subsequently. Other molecular data help demonstrate that *Schistosoma* is indeed

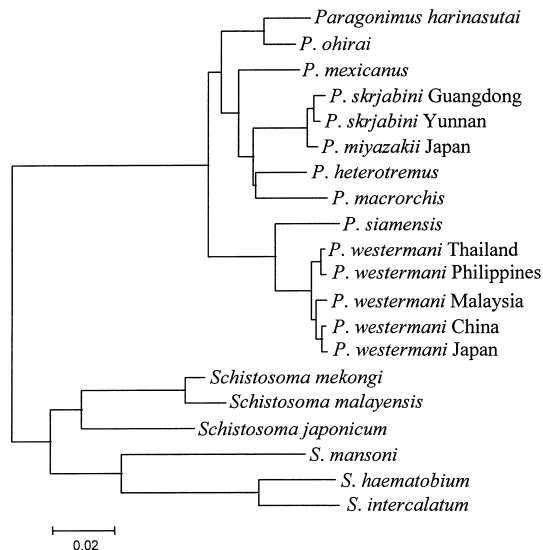


Fig. 3. Distance tree showing relationships of *Schistosoma* and paragonimid species based on 372 bp of the mitochondrial *cox1* gene. Analyses in DAMBE (Xia, 2000) indicated that the sequences were not saturated with transversions. Consequently, a transversion distance matrix was constructed in MEGA2 (Kumar *et al.* 2000) using the Kimura 2-parameter model and a tree constructed using the minimum evolution method. Divergence depths are far greater among members of the genus *Schistosoma* than among paragonimids. Note that some relationships among paragonimids differ from those in Fig. 4.

very ancient. Our analyses of sequences of a 372 bp fragment of DNA from the mitochondrial *cox1* gene from a number of schistosomatids and paragonimids (Fig. 3) suggested that they were not saturated with transversions (see caption to Fig. 3). The sequences might therefore provide a reasonable phylogeny of the two groups and a relative indication of divergence times. Examination of the relative depths of nodes in the tree (Fig. 3) implies that the divergence in *Schistosoma* is much older than in *Paragonimus*. Of course, caution must be exercised in interpreting such a tree: rates of evolution might differ in the two lineages. Nevertheless, given that *Paragonimus* has a typical Gondwanan distribution, the implication is that *Schistosoma* diversified well before the break-up of Gondwana.

The dispersal hypothesis places the ancestral home of *Schistosoma* in Asia (Snyder & Loker, 2000 and reviewed in Morgan *et al.* in this supplement), with subsequent dispersal into Africa in the Miocene/Pliocene. The strength of this hypothesis is its agreement with the topology of molecular trees showing early-diverging taxa to be in Asia. There are also some weaknesses. The relative depths of branching of *Schistosoma* and *Paragonimus*, shown in Fig. 3, have already been mentioned. The supporters of the Asian-origin hypothesis did not specify an exact region of origin. Wherever the genus arose, its

members would have had to disperse into both India and Africa. The ramparts of mountains thrown up by the collision of the Indian plate with Asia would have made colonisation of India by existing Asian freshwater fauna difficult. With regard to Africa, the Tethys Sea separated this continent from Asia until probably as recently as 5–10 MYa (Smith, Smith & Funnell, 1994). The sea was most likely shallow and narrow, but would nevertheless have been a barrier to terrestrial species (but see Cox, 2000). If *Schistosoma* species did first enter Africa in the Miocene/Pliocene, then they must have diversified extremely rapidly on that continent. In particular, as mentioned above, members of the *S. haematobium* group must have radiated across Africa in a wide range of snail species from the ancient bulinine lineage in a relatively short space of time.

One more element of the debate about the radiation of *Schistosoma* species and their hosts needs to be touched on. *Schistosoma mansoni* now occurs in both Africa and South America. Although Davis (1979) originally proposed that this was a consequence of ancient vicariance, recent molecular evidence (Després *et al.* 1993) is more consistent with a human introduction of the parasite from Africa during the slave trade several centuries ago. However, the story concerning the snail hosts cannot be so simple. Like the schistosome, the planorbid genus *Biomphalaria* occurs in both Africa and South America. One South American species, *B. glabrata*, is more similar, both morphologically and genetically, to African species than to other South American species (Pilsbry, 1911; Woodruff & Mulvey, 1997; Campbell *et al.* 2000). Two classes of explanation exist. One is that *Biomphalaria* species were already diverse in Gondwana before the separation of Africa and South America and the observed relationships are therefore due to vicariance (Davis, 1979, 1980). The other explanation is that the genus diversified in the Americas and dispersed to Africa, probably during the Pliocene (Woodruff & Mulvey, 1997; Campbell *et al.* 2000). Fossils are known from the Americas at least as far back as the Paleocene (South America – Parodiz, 1969) and Oligocene (North America – Pierce, 1993). According to Woodruff & Mulvey (1997), fossils of *Biomphalaria* are not known before the mid-Pleistocene in Africa. However, this overlooks reports of relevant planorbid fossils from the Fayum of Egypt in the upper Cretaceous (Newton, 1920).

Molecular data used to infer a recent dispersal of *Biomphalaria* from South America to Africa (e.g. Woodruff & Mulvey, 1997; Campbell *et al.* 2000) also imply that divergences among South American species are very recent, a scenario not consistent with the existence of fossils over 50 MY old. This problem is particularly apparent in the COI data reported by Campbell *et al.* (2000). Based on an average rate of change of COI genes, they suggested that the

ancestor of African *Biomphalaria* species dispersed to Africa not more than 3·6 MYa. Although they did not report estimated dates of divergence between *B. glabrata* and other South American species, their Fig. 2b implies that such divergences could hardly have been more than 5–10 MYa. This discrepancy needs to be investigated further, and additional South American taxa included in future studies.

Despite the case made for this by Woodruff & Mulvey (1997) and Campbell *et al.* (2000), it is hard to imagine freshwater pulmonates dispersing such great distances across an ocean. If snails were able to do so, then there should be evidence that other freshwater or terrestrial animals of similar size have also made the passage. No generalised track for such animals has a recent west to east dispersal over the ocean between South America and Africa (Croizat, 1958).

Knowledge of the origins of *Schistosoma* and its species is essential if we are to understand the association of *Schistosoma* and its snail hosts through time. The Gondwanan-origin hypothesis is more parsimonious in emphasising extensive phylogenetic congruence of parasites and snails, although there must have been a host switch at some stage between planorbid and lymnaeid hosts, and another between pulmonates and pomatiopsids. The Asian-origin hypothesis not only requires the host switches mentioned above, but also implies additional and extensive host-switches and host additions, albeit at relatively low taxonomic levels, as *Schistosoma* species entered Africa and diversified. Unless all hosts disperse together with their parasites, dispersalist scenarios such as this will always require more instances of host extension to explain them and will therefore seem less parsimonious.

The switch from pulmonates to pomatiopsids by the ancestor of the *S. japonicum* and *S. sinensium* groups is important. This seems to be a clear case of host switching and was a pronounced departure for pulmonate-dominated *Schistosoma*. This host switch is puzzling given the ubiquity of pulmonates. However, if the Gondwanan-origin hypothesis is correct, geological events might provide an explanation. As the Indian Plate moved towards Asia it passed over an active centre of volcanism that obliterated life over much of southern and western India and created the Deccan Traps (Davis, 1979). Such an event might have eliminated pulmonates locally. This, coupled with the ecological revolution caused by the rapid Himalayan orogeny that created new environments, could have promoted host-switching.

The *S. japonicum* species complex consists of three species in east and southeast Asia. The best known species, *S. japonicum*, occurs in *Oncomelania* over a large geographic area that includes China, Japan, Sulawesi and the Philippines. The remaining two species (*S. mekongi* and *S. malayensis*), almost

identical to *S. japonicum* in morphology of all stages, including the egg, occur in triculines and have limited distributions. The divergence among these species must date to the Miocene separation of the snail subfamilies some 10 million years ago. Davis & Greer (1980) predicted, on the basis of snail systematics, distribution and timing of river formation and direction of evolution of the Pomatiopsidae in time and space, that the two triculine-transmitted schistosomes would be more closely related to each other than either is to *S. japonicum*. With the advent of molecular data for the schistosomes (Blair *et al.* 1997b) this has been confirmed. There is complete congruence between the area cladograms for river formation, snail phylogeny and *S. japonicum* group phylogeny based on molecular data. The *S. japonicum* group therefore seems to constitute a limited radiation in allopatry.

Schistosoma mekongi is transmitted in a small portion of the lower Mekong River by only one species of *Neotricula* (Tribe Pachydrobiinae) that is sympatric with numerous genera and species of the same tribe and the sister tribe Juliini. *Schistosoma mekongi* will not develop in any other pomatiopsid snail (experimental infections reviewed in Davis, 1980, 1992). *Schistosoma malayensis* is found in rainforests in a small region of Malaysia where Davis & Greer (1980) discovered the snail host by deliberately looking in the correct ecological setting for the sister taxon to *S. mekongi* in a triculine snail. They found the snail and parasite and described *Robertsia*, a sister genus to *Neotricula*. That there are only two species transmitted by triculines within the *S. japonicum* group may seem puzzling given the enormous radiation of the host subfamily. However, *S. mekongi* and *S. malayensis* were described as distinct species only within the last two decades and only after it was discovered that triculine snails transmit *Schistosoma* spp. (see Davis, Kitikoon & Temcharoen, 1976). We suspect that more species will be discovered as causative agents of human schistosomiasis in Asia are investigated more critically.

Associated with the Triculinae is an unusual schistosome, *Schistosoma sinensium*. This nominal species infects rodents and has eggs reminiscent of those of *S. mansoni*. Davis (1992) considered it to represent a complex of at least three species in Thailand and China that is a sister to the *S. japonicum* complex and evolved from an early ancestor on the Indian Plate. Molecular data from two populations of *S. sinensium* have shown these to be very distinct from one another and that they do indeed form a sister clade to the *S. japonicum* group (Agatsuma *et al.* in press a). Although little is yet known about this group, it appears to resemble the *S. japonicum* group in constituting a limited radiation in allopatry despite the vast radiation experienced by the host group. As suggested above for the triculine-

borne members of the *S. japonicum* group, discovery of further taxa in the *S. sinensium* group is likely.

The Paragonimidae

Sister taxa for the paragonimids have not been identified with certainty. All paragonimids, where known, parasitise caenogastropods of the superfamilies Cerithioidea and Rissooidea (Fig. 1). Likely sister families, according to Odening (1974) are the Troglotrematidae (in which paragonimids are sometimes placed) and the Nanophyetidae. Snail hosts are known for only two species in the former family and are rissooidean amnicolids (genus *Bythinella*) in each case. Hosts for the latter family include *Semisulcospira*, *Juga*, *Oxytremata* (cerithioideans) and *Campeloma* (ampullarioidean). Species of *Paragonimus* and *Euparagonimus* fall into two clades in Fig. 4. One utilises cerithioidean snails, the other rissooideans. If nanophyetids and troglotrematids are valid sisters, then the earliest paragonimids could have utilised either cerithioidean or rissooidean snails.

One of the two clades contains *P. westermani* and the closely related *P. siamensis* as well as (tentatively) the genus *Euparagonimus* (Fig. 4). *Paragonimus westermani* uses cerithioidean snails and we have inferred that this is also the likely host group for *Euparagonimus cenocopiosus* (unpublished). Yaemput, Dekumyoy & Visiassuk (1994) proposed that the host for *P. siamensis* is the viviparid *Filopaludina martensi*, a member of another caeno-

gastropod superfamily, the Ampullarioidea. This is unlikely given the host relations of other members of the clade, but not impossible. The second main clade contains all remaining *Paragonimus* species, all of which utilise rissooidean snails.

One of the paragonimids in the east Asian radiation utilising pomatiopsids requires special mention. '*Paragonimus skrjabini*' in China must represent a complex of very closely related taxa at or below the level of species. Barring misidentification of cercariae, at least 33 nominal species of triculine and amnicolid snails have been reported as hosts (Davis *et al.* 1994; Wilke *et al.* 2000). Ecological factors and/or isolation have probably led to extensive allopatric radiations of the snails, especially the triculines, and Davis *et al.* (1999) suggested that 50% of the relevant species have yet to be described. Genetic differences exist among geographically distinct populations of the parasite (Blair *et al.* unpublished), presumably mirroring the situation among the snail populations. We are probably seeing incipient allopatric speciation in the *P. skrjabini* group as a consequence of cospeciation with the diverging host snails.

We can now also identify an instance of host addition or switching in the *P. skrjabini* group. The defining situation was the discovery in Fujian, China, of putative *P. skrjabini* transmitted in micro-sympatry by two snail species, one a species of *Tricula* (Pomatiopsidae: Triculinae), the other a species of *Erhaia* (replaces *Pseudobythinella* as used in China, a junior homonym of an English fossil rissooidean taxon; see Davis & Kang, 1995), until recently classified in the Pomatiopsidae (e.g. Davis *et al.* 1999) but now, on the basis of molecular data, assigned to the Amnicolidae (Wilke *et al.* 2000). Species of *Erhaia* range from northern India into Yunnan, Hubei, Hunan and Fujian Provinces in China. They are similar in size (very small) and choice of habitat (small mountain streams) to species of *Tricula* and some other triculine genera. Molecular data involving DNA sequences of three genes have shown not only that *Erhaia* is an amnicolid but also that it is closely related to *Moria* in Japan (Wilke *et al.* 2000) that also transmits a species of *Paragonimus*. We are currently attempting to obtain molecular information on the *Paragonimus* species utilising these different hosts in Fujian. If two different sibling species of parasite are involved, then the field observations are best interpreted as a host switch. If a single form of *P. skrjabini* occurs in both snails, this is an example of host addition. In either case it is interesting that the host extension has been to an available rissooid-grade snail in the very limited ecological setting necessary for the transmission of *P. skrjabini*.

Amnicolid snails were able to colonise the southern parts of the Japanese archipelago while triculines did not. *Paragonimus miyazakii* is transmitted in Japan

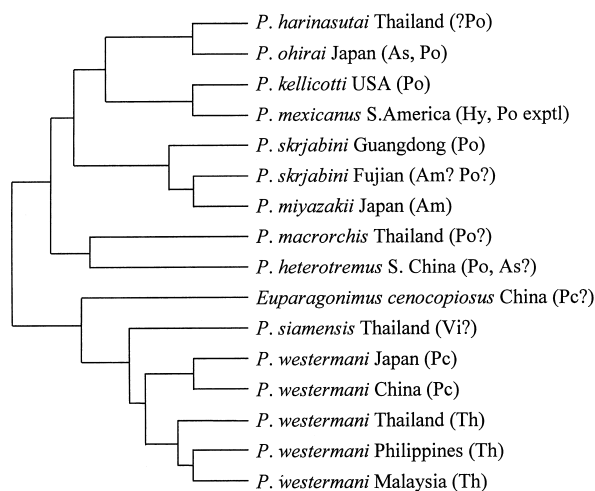


Fig. 4. Phylogeny (cladogram) of the Paragonimidae based on recent molecular studies by Blair and co-workers. The tree is a summary of data from two gene regions, the mitochondrial *cox1* gene and the nuclear second ribosomal internal transcribed spacer. The tree is midpoint-rooted. Localities are indicated. Snail families are as follows: Am, Amnicolidae; As, Assimineidae; Hy, Hydrobiidae; Pc, Pleuroceridae; Po, Pomatiopsidae; Th, Thiaridae; Vi, Viviparidae. A question mark (?) indicates a tentative host assignment.

by the amnicolid genus *Moria*. Available molecular data are unambiguous in placing *P. miyazakii* as a close sister to *P. skrjabini* (see Blair *et al.* 1999). Furthermore, sequences from at least one form of nominal *P. skrjabini* from Fujian are more similar to those of *P. miyazakii* than they are to nominal *P. skrjabini* from southwestern China. Various scenarios leading to this situation can be imagined. For example, a Chinese population of '*P. skrjabini*' might have extended its range to Japan by capturing an amnicolid host there, diverged in allopatry to become *P. miyazakii*, and subsequently re-established in China in *Erhaia* in sympatry with local *P. skrjabini*. However, any acceptable interpretation must await more data.

Molluscan host relations in *Paragonimus westermani* (Fig. 4) probably provide another example of host addition. *Paragonimus westermani* populations in east Asia utilise pleurocerids and those in southeast Asia utilise thiarids. At first glance, these relations might be taken as an example of phylogenetic tracking with host taxa and parasite taxa associated since the origins of both. However, relative taxonomic levels of parasite (species or species group) and host (family) argue against this. Host-addition as defined earlier, followed by genetic divergence towards speciation in allopatry, appear to offer a better explanation. Molecular genetic studies show that populations of *P. westermani* utilising thiarid snails (that arrived in southeast Asia via a generalised track from Africa–India) and those utilising pleurocerids (coming from North America along a generalised track into Japan–Korea to Taiwan and southern China) are now as distinct from each other as are a number of other species in the genus (Blair *et al.* 1997a). Host addition is characterized by allopatric distributions of the host taxa. Thiarids and pleurocerids are both distributed widely but their range of overlap is limited to parts of southern and southwestern China. Other examples of probable host addition may be seen among paragonimids. For example, the widespread species *P. ohirai*, occurring in both fresh and brackish waters of coastal east Asia, uses several host species within the families Assimineidae and Pomatiopsidae. These host species do not co-occur in any locality where *P. ohirai* is found. Experimental infections can extend the snail host range of *P. ohirai* to include several pomatiopsids not known to be natural hosts, including an American species, *Pomatiopsis lapidaria* (reviewed in Blair, Xu & Agatsuma, 1999).

SYNTHESIS

Although phylogenies of schistosomatids and paragonimids appear to exhibit broad congruence with those of their snail hosts, there are differences between the two families of digeneans, notably in the frequency of host additions. For the Schisto-

somatidae as a whole, phylogenetic tracking seems to explain the patterns of host usage (Fig. 2). There may have been switches among lymnaeids, physids and planorbids, often apparently at a shallow phylogenetic level with respect to parasites. It is understandable that switches might occur among related families such as these (all within the Basommatophora), which presumably have a high degree of genetic similarity. Nevertheless, there have also been longer-range switches on at least two occasions into marine gastropods, and a wide range of marine families have been exploited (Figs 1, 2), although generally only by a single species or genus in each case. The processes driving this are discussed below. Within *Schistosoma*, the situation is confused by uncertainty about the origins and evolution of the genus. Association with pulmonates is evident, but the extent of host switching implied will depend on which evolutionary model for the genus is accepted. One major host switch, between a pulmonate and caenogastropod has certainly occurred, as discussed earlier. Host addition beyond the level of a single snail genus is not apparent in schistosomatid species with the possible exception of members of *Austro-bilharzia*.

In *Paragonimus*, various host switches at the level of family or superfamily can also be observed (Fig. 4). Basal in the family, there must have been a switch between a cerithioidean and a rissooidean host (assuming that both superfamilies were in existence before the evolution of *Paragonimus*). Thereafter, all paragonimids remained faithful to hosts of the same grade of organisation (cerithioideans or rissooideans) and did not exhibit switches over vast phylogenetic spans as schistosomatids did. One large clade remained faithful to pomatiopsids in Asia, but switched to another rissooidean family in Central/South America. (Rissooideans hosting *Paragonimus* species in Central and South America should probably be referred to the family Cochliopidae rather than to the Hydrobiidae as is customary: Davis unpublished.) Unlike the situation for single species or species complexes of schistosomatids, clear host additions by single paragonimid species or complexes are observed at the level of host family. Within the *P. skrjabini* group, amnicolid snails have been added to the usual pomatiopsid hosts. *Paragonimus ohirai*, for which pomatiopsids are presumably plesiomorphic hosts, can now utilise both pomatiopsids and assimineids within a small geographical area. Within the *P. westermani* group, two different cerithioidean families are used, indicating another addition event.

Another difference between *Paragonimus* and *Schistosoma* concerns the extent of radiations in a given geographic area. A relatively large number of closely related *Paragonimus* species occur in east Asia (Blair, Xu & Agatsuma, 1999). Many of these utilise pomatiopsid snails and some occur in sympatry

where they may utilise the same snail species (yet to be confirmed). This might represent an adaptive radiation. However, we are mindful of the difficulties of confirming the 'adaptive' aspect of a radiation. The term 'evolutionary radiation' might be more appropriate (Futuyma, 1998). This pattern of distribution and host use is quite different from that seen in, for example, the *Schistosoma japonicum* group. The three known species in the *S. japonicum* group do not overlap geographically or in host use and probably represent a limited radiation in allopatry. If members of the *S. japonicum* group have tracked the pomatiopsids, many instances of parasite extinction, or of 'missing the boat' (Paterson & Gray, 1997), must be postulated: there are three schistosome species, each utilising one snail species, and at least 120 pomatiopsid species in east Asia, all but two belonging to the Triculinae. However, ecological factors, discussed below, might help explain the abundance of schistosome-free pomatiopsid species.

Given that host-extension is possible, why have schistosomatids and paragonimids 'chosen' the species they have? All else being equal, we should expect a parasite to involve a closely related host in a host switch/addition. Another important factor is ecological opportunity. For example, the *Paragonimus skrjabini* complex has added to its snail hosts the amnicolid *Erhaia*, a genus ecologically very similar to its widespread triculine hosts. Similarly, *Semisulcospira* (Pleuroceridae) and *Brotia* (Thiaridae), both hosts for *Paragonimus westermani* in different parts of Asia, are similar in their habitat preference and ecology. Ecological factors may also prevent certain phylogenetically-appropriate snails from acting as hosts. Successful transmission of a digenean requires a setting where the definitive host can become exposed to infection. For example, the reason why members of the enormous radiation of Stylommatophora are impervious to infection is, simply, that they are all terrestrial. Schistosomatid transmission requires an aquatic environment for miracidia and cercariae. The triculine radiations of the Pachydrobiini and Jullieniini fill every conceivable ecological niche in rivers or in deep lakes, niches unavailable to potential mammalian hosts. Thus, most triculines are ecologically removed from schistosome transmission.

We need to ask why so few schistosomatids and no paragonimids occur in strictly marine habitats. Of the approximately 22 families of freshwater snails worldwide (Davis, 1982; Wilke *et al.* 2000), schistosomatids and paragonimids both utilise about six. In the case of paragonimids, the families are scattered throughout the Cerithioidea and Rissosoidea, both superfamilies that also contain many marine families. The phylogenetic range of schistosomatid hosts in freshwater is even greater, encompassing both heterobranchs and caenogastropods (Fig. 1). There

are therefore no absolute phyletic constraints preventing colonisation of marine gastropod taxa by these parasite families. The explanation for their restriction to freshwater habitats is more likely to be that the physiology of the parasites, or host specificity with regard to non-molluscan hosts, is responsible. When a switch to a marine host has been made, the host family exploited is often phylogenetically removed from freshwater host families. For example, *Paragonimus ohirai* utilises the family Pomatiopsidae in freshwater habitats, but populations cycling through brackish water habitats exploit assimineid snails. Where multiple marine families are used by a single schistosomatid genus, they can be unrelated to one another, suggesting multiple colonisations. For example, species of *Gigantobilharzia* generally occur in planorbids in freshwater but one, *G. huttoni*, utilises a marine opisthobranch and cercariae ascribed to this genus have been found in the brackish-water snail *Hydrobia stagnalis* (Rissosoidea). (Note, however, that there is confusion concerning this name which probably refers to a member of the Hydrobiidae, but has also been used for a species within the Cochliopidae). Cercariae of *Austrotilharzia* have been reported from five families of marine snails in three superfamilies (Fig. 1). The marine species into which schistosomatids have switched generally occur in huge numbers in shallow and intertidal coastal areas where the avian definitive hosts are abundant. Ecology and opportunity are presumably linked here and phylogeny is of less importance in the selection of snail host.

It might be expected that a switch into a new host lineage and habitat would open up new opportunities for a parasite lineage and that a radiation would ensue. This does not seem to be the case with *Austrotilharzia* + *Ornithobilharzia* which today constitutes small group of about 10 recognized species (Basch, 1991). This is not a large number considering the opportunities that the marine habitat would seem to offer and the high densities of snails found in many inshore localities. However, the relevant bird hosts are highly vagile: their ability to traverse the globe might militate against parasite speciation. Even in freshwaters, where habitats are fragmented and hosts less vagile, extensive radiations are not seen in schistosomes. Neither the *S. japonicum* group nor the *S. sinensium* group has yielded more than a handful of known species despite their geographic ranges and the extensive radiations experienced within a similar time frame by the snail host groups.

One family of snails, the Pomatiopsidae (range also includes North America), is host to both schistosomatids and paragonimids. It may be that this family is particularly permissive as a host for digeneans and hence unusually prone to host extension. In particular, the genus *Oncomelania* appears to be a permissive host for many species of *Paragonimus* to which it is not normally exposed

(reviewed in Blair, Xu & Agatsuma, 1999). Japanese *Oncomelania hupensis nosophora* is susceptible to experimental infection by two American species, *P. kellicotti* (normal host *Pomatiopsis lapidaria* also in the Pomatiopsidae) and *P. mexicanus* (normal host *Aroapyrgus* spp. in the Hydrobiidae *sensu lato*). Only a small proportion of snails yielded mature infections in the latter case. Asian species for which *O. hupensis nosophora* can act as an experimental host include *P. ohirai* (see above), *P. miyazakii* (normal host in the Amnicolidae) and *P. heterotremus* (normal hosts also in the Pomatiopsidae). The American species *P. lapidaria* is also permissive for *S. japonicum*. Further studies on the digenean faunas of pomatiopsids might provide valuable data for those interested in host specificity and host extension.

The absence of parasite species-specific internal defence mechanisms in snails may mean that digeneans are not bound by restrictions imposed by a coevolutionary arms race. Consequently, it may be easier than previously assumed for digeneans to switch to host taxa with convergently similar defence mechanisms (Adema & Loker, 1997), or indeed, to host taxa with similar ecologies but not necessarily similar phylogenies. Our thinking about the evolutionary interactions of digeneans and snails has been heavily influenced in the past by assumptions of strict coevolution. Many studies on coevolution have focused on vertebrates that have immune systems able to focus on individual species of pathogen. We predict that coevolutionary studies on invertebrates (and plants) and their parasites/associates will find many examples of phylogenetic tracking rather than strict coevolution. The extent of reciprocal evolutionary responses by the host against any particular associate will depend on the relative prevalence of that associate.

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