

INVITED REVIEW

Parasites as to Host Evolutionary Prints: Insights into Host Evolution from Parasitological Data

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Abstract—Thomas F., Verneau O., De Meeûs T. & Renaud F. 1996. Parasites as to host evolutionary prints: insights into host evolution from parasitological data. *International Journal for Parasitology* 26: 677–686. The close relationships which link parasitic organisms to their hosts have led to the use of parasites as biological tags. Most studies on this topic refer to parasites as host ecological tags. Recent development of molecular methods which give access to the genomic structures of populations have provided new information on the evolutionary biology of parasites. In this paper, we have attempted to review whether parasites can be considered as “host evolutionary prints”, and focus our discussion on host biodiversity and biogeography. Copyright © 1996 Australian Society for Parasitology. Published by Elsevier Science Ltd.

Key words: Host–parasite relationships; evolution; biodiversity; biogeography; biological tags.

INTRODUCTION

Increasingly, parasitism is considered a major factor which has influenced the organisation and evolution of life. Indeed, for most host–parasite associations, current relationships appear to reflect “coevolution” between 2 genomes (i.e. those of the host and the parasite) over time. Many studies now attempt to analyse the role of parasites in the structure of host biodiversity and in the evolution of host life histories. The strict dependence of the parasite on its host and the exploitation of the latter by the former provide an ideal model for investigations in the fields of ecology and evolutionary biology. For more than 50 years, we have known that parasites can provide information on the ecology and ecosystems of their hosts. Thus, parasites have often been considered to be biological tags particularly in studies on population biology (see review by MacKenzie, 1986). For instance, parasites have been

used frequently to investigate the existence of fish stocks, assuming that geographic variation in parasite abundance and/or richness reflects patchiness of the host population (Sindermann, 1961; Gibson, 1972; Wickins & MacFarlane, 1973; McGladdery & Burt, 1985; Scott, 1985; Butorina & Shedko, 1989; MacKenzie, 1990; Bower & Margolis, 1991; Rohde, 1987; Moser & Hsieh, 1992). When parasites are localised in a particular geographical area, they can be used successfully to localise the nursery grounds of several fish species (Olson & Pratt, 1973; Bouillon & Dempson, 1989). Because many parasite species exploit food webs of the specific hosts to complete their life cycles, differential rates of infection may reflect the feeding habits of the host (McGladdery & Burt, 1985; Rydlo, 1985; Aura, Valtonen & Andersin, 1990; Zhokhov & Kasyanov, 1995). These parasitological data also lead to comparisons between the ecology of sympatric host species (Lile, 1992). Parasites have also been used in more specific ecological studies such as the analysis of parasite biodiversity and host movements after a fire (Torres *et al.*, 1992).

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Because stress factors such as pollution often lead to an increase in host susceptibility, parasites have been used as indicators of environmental conditions (Wedemeyer & Goodyear, 1984; Turner, 1985). More generally, interspecific, intraspecific, and inter-individual variation in parasitic infections may correlate with environmental, demographic, behavioural and human variables (Stuart & Strier, 1995).

The large number of ecological studies which use "parasitological methods" reflects the fact that parasites are suitable tools with which to investigate host ecology. However, little attention has been devoted to the potential value of parasites as "host evolutionary prints." By this, we mean that information obtained from a study of the parasites in or on a given host provides new data concerning the evolutionary biology of that host. The recent advances in genetic and molecular methods provide new sets of data which reveal hitherto unknown information about the evolutionary history of host-parasite associations. In this paper we will try to present cases in which a parasite taxon constitutes a host evolutionary print. Particularly, we will attempt to focus our analysis on host biosystematics, biogeography, phylogeny and hybrid zones.

HOST BIOSYSTEMATICS AND BIOGEOGRAPHY

The taxonomic power of parasites was mentioned by Ernst Mayr himself who is the founder of the biological species concept. Mayr (1974) noticed that 2 sibling species of *Octopus* (Cephalopoda) were distinguished by the specific dicyemid parasites that they harboured. Indeed, many parasites display a narrow specificity to their host species. Therefore, these parasite taxa can only develop successfully in/on one host species. This characteristic makes them excellent taxonomists of the host group (Lambert & El Gharbi, 1995). Recent analyses on parasite systematics have led to a reconsideration of host systematics. For example, Euzet, Agnese and Lambert (1989) tested the value of gill monogeneans as systematic indicators of their fish hosts. Their anatomical study of parasites revealed the existence of 6 distinct species; the specific associations of 2 parasite species have permitted the distinction of 3 host groups. In other words, the occurrence of 2 species of parasites is sufficient to define a host group. A genetic analysis (i.e. isozyme loci) performed on these 3 host groups showed a strong correspondence with the systematic analysis suggested by the parasites (i.e. the 3 host groups are 3 biological species). The same kind of approach is proposed by Paugy, Guegan & Agnese (1990) who made a genetic analysis of 2 cyprinid

populations following the discovery of 2 host-specific Monogenea. Indeed, the genetic analysis confirmed the existence of 2 host species.

Analysis of the richness and distribution of copepod communities within and between different geographic areas have led Kabata and Ho (1981) to discuss the origin and dispersal of fishes belonging to the genus *Merluccius* (Teleostei, Gadidae). Indeed, parasite specificity and distribution may currently reflect paleoevents which have governed host evolution. Until recently, the genus *Trisopterus* (Teleostei, Gadidae) was considered to comprise 3 species in the Atlantic Ocean and in the Mediterranean Sea: *Trisopterus luscus* and *Trisopterus minutus minutus* in the Atlantic and *Trisopterus minutus capelanus* in the Mediterranean. We know that the Mediterranean Sea was colonised by Atlantic fauna during several geological periods (see Quignard, 1978 for fishes; Zachariasse & Spaak, 1983 for Foraminifera) and consequently, *T. m. capelanus* has been considered a subspecies of *T. m. minutus*. Since only a single species of the genus *Diclidophora* (Monogenea) which parasitizes the genus *Trisopterus* was known from anatomical investigations, Tirard *et al.* (1992) performed a genetic study of populations located on both sides of the Strait of Gibraltar to define divergences between these helminth populations. A first analysis of the multilocus structure (i.e. 11 isozyme loci) of *Diclidophora*, which parasites 2 sympatric populations of *T. luscus* and *T. m. minutus* in the Atlantic Ocean, revealed the existence of 2 parasite species which were specific to each of the 2 hosts. Furthermore, a strong genetic similarity was found between monogeneans parasitizing *T. luscus* in the Atlantic Ocean and those parasitizing *T. m. capelanus* in the Mediterranean Sea (Table 1). Because parasites can often be considered "excellent taxonomists" of the host taxon which they parasitize, the results obtained for the genetic structure of the genus *Diclidophora* led to a re-examination of the systematics of the 3 host taxa belonging to the genus *Trisopterus*. A second study based on the analysis of the multiloci structure (i.e. 16 isozyme loci) of 3 populations of *T. luscus*, 2 populations of *T. m. minutus* from the Atlantic Ocean, and 1 population of *T. m. capelanus* from the Mediterranean Sea, revealed a high genetic divergence between the 2 subspecies (i.e. between *T. m. minutus* and *T. m. capelanus*) on one hand, and a strong genetic similarity between *T. luscus* and *T. m. capelanus* on the other hand (Tirard *et al.*, 1992). Table 1 also shows the genetic distances calculated between the 3 teleostean taxa. It is obvious that *T. m. capelanus* does not represent the Mediterranean subspecies of *T. m. minutus* (Fig. 1).

Table 1—Gregorius (1984) genetic distances between 3 taxa of *Diclidophora* (Monogenea), and between the 3 taxa of their specific Teleost hosts (Gadidae)

	<i>Diclidophora minuti</i> (<i>Trisopterus minutus minutus</i>)	<i>Diclidophora luscae</i> (<i>Trisopterus luscus</i>)	<i>Diclidophora</i> (<i>T.m. capelanus</i>)
<i>Diclidophora minuti</i> (<i>T. m. minutus</i>) Atlantic Ocean	—	0.45	0.33
<i>Diclidophora luscae</i> (<i>Trisopterus luscus</i>) Atlantic Ocean	0.45	0.57	0.58
<i>Diclidophora</i> (<i>T.m. capelanus</i>) Mediterranean Sea	0.57	—	0.1
	0.33	0.13	—
	0.58	0.1	—

The Gregorius genetic distances (Gregorius, 1984) result from the analysis of 11 and 16 isozyme loci for parasites and hosts respectively (data from Tirard *et al.*, 1992). These distances are between 0 and 1. The distances between host teleost taxa are represented in bold.

The analysis by Tirard *et al.* (1992) of helminth populations has thus made it possible to reconsider the evolutionary history of their host groups, and reveals mistakes committed in the past in the study of morphological and anatomical characters of the host. Thus, Stevidov (1948) considered that the *Trisopterus* in the Mediterranean was a subspecies of *Trisopterus minutus* from the Atlantic Ocean. These morphoanatomical characteristics, which were a source of error for ichthyologists, must be ascribed to convergences between *T. minutus* (Atlantic) and *T. luscus* (Mediterranean). So, *T. luscus* has colonised the Mediterranean Sea, whereas *T. minutus* is not mentioned in this geographical area (Fig. 1). The paleogeographic hypothesis proposed by Tirard *et al.* (1992) is in complete agreement with what is observed for the genetic structure of *Diclidophora*, the monogenean parasites of these teleosts. This approach demonstrates once again the advantages of the simultaneous study of both hosts and parasites for an understanding of the evolutionary processes which govern host-parasite interactions.

Concerning the same host family, Tirard *et al.* (1993) made another genetic study on their copepod parasites of the genus *Lernaeocera*. The results show that it is *L. lusci* which parasitizes *T. m. capelanus* in the Mediterranean Sea, and not *L. branchialis* as previously described (Delamare-Deboutville, 1950). So the distribution of *L. Lusci*, and that of its host, *T. luscus*, must be extended to the Mediterranean Sea. The information obtained from these copepods agrees completely with that obtained previously from the monogeneans and confirms the role of parasites as host evolutionary prints. Moreover, the study on *Lernaeocera* from the Mediterranean and the Atlantic coasts also revealed that host-switching occurred in the Mediterranean. Indeed, another gadid (i.e. *Merluccius merluccius*) which was not parasitized

in the Atlantic, became the major host of *L. lusci* in the Mediterranean. Thus, it is possible that this transfer of *L. lusci* into a new host resource might be related to biological modifications undergone by its host (i.e. *T. luscus*) in its new environment (i.e. Mediterranean Sea). Thus, this differential specificity displayed by *L. lusci* between the Atlantic and Mediterranean may reveal divergences covering several aspects of the biology (i.e. growth, reproduction, life-span) between the Atlantic (Labarta *et al.*, 1975) and the Mediterranean (Planas & Vives, 1952; Froggia & Zoppini, 1981) populations of *T. luscus*.

In a biogeographical and evolutionary context, studies on Cestodes show a strange situation. Species belonging to the genus *Bothriocephalus* which parasitize teleost fishes display a narrow specificity to their host species (Renaud, Gabrion & Pasteur, 1983; Renaud & Gabrion, 1984). An initial genetic analysis conducted between populations of 2 of these species of parasites in 2 geographical areas (i.e. the Atlantic Ocean and the Mediterranean Sea) revealed a high genetic divergence within 1 tapeworm species. Indeed, whereas differences were encountered between populations of *Bothriocephalus barbatus* parasitizing the brill, 5 enzymatic loci among 11 studied presented different fixed alleles between the 2 populations of *B. gregarius* parasitizing the turbot (Renaud, Gabrion & Pasteur, 1986). In order to understand the geographical boundaries of these 2 genetic entities of *B. gregarius*, a second study was undertaken along the European coasts. The results showed a surprising situation because 1 genetic entity of these tapeworms appeared to be sandwiched between the other one (Fig. 2). Thus, turbot harboured 2 geographical taxa of *B. gregarius* (see Renaud, Blanquer & Gabrion, 1990). To explain this, a genetic study was conducted on turbot populations. No difference could be found during this analysis,

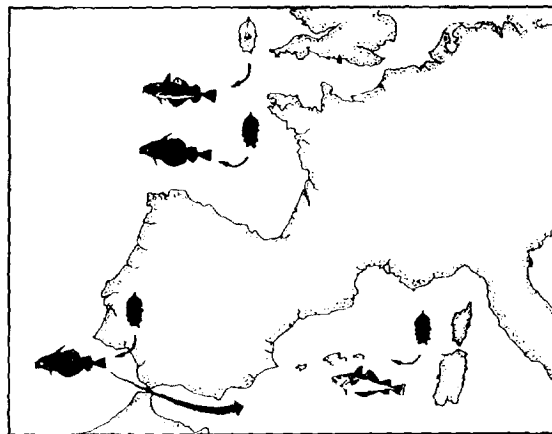
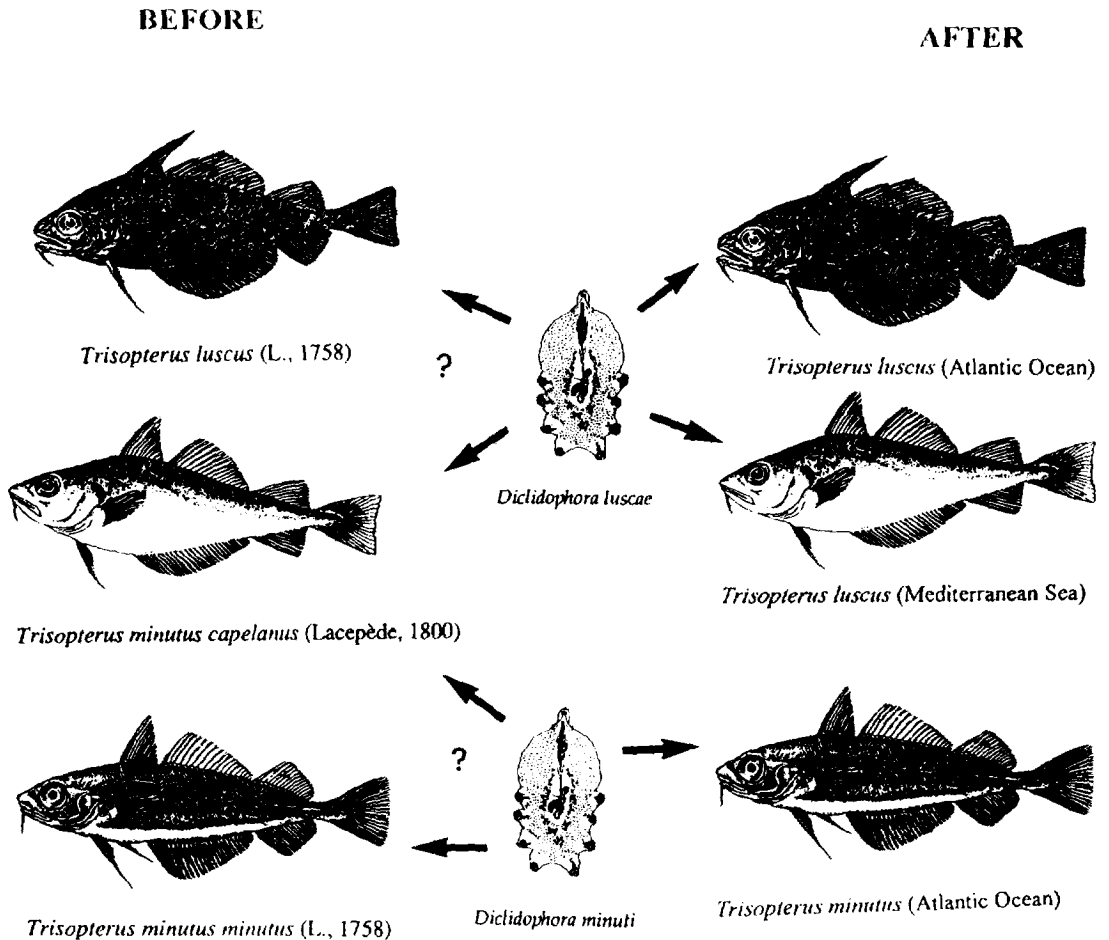


Fig. 1. Taxonomic position of different gadoid fishes **before** and **after** the biosystematic analysis of their monogenean parasites. First, the genetic study on parasites revealed the existence of 2 parasite taxa (*Diclidophora luscae* and *D. minuti* n. sp.). The specificity of these 2 parasite species and their geographical distribution has led to a re-examination of the systematic position of their hosts. It was thus demonstrated that parasites are excellent taxonomists, because *Trisopterus minutus capelanus* belongs to the same genetic entity as *T. luscus*. The map shows the migration of *T. luscus* with *Diclidophora luscae* in the Mediterranean Sea which led to the situation observed currently.

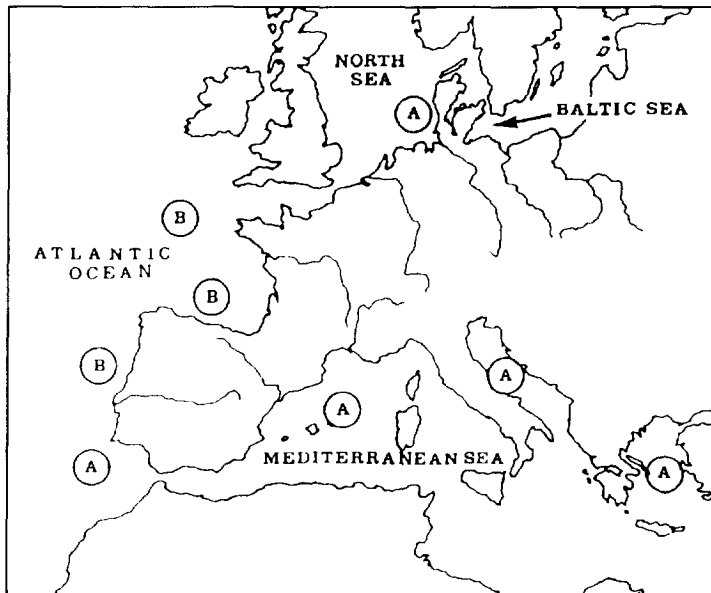


Fig. 2. Map showing, the geographical distribution of the 2 genetic entities of *Bothrioccephalus gregarius* (i.e. genetic entities A and B see Renaud, Blanquer & Gabrion, 1990).

suggesting a strong genetic homogeneity within this host taxon (i.e. turbot) (see Blanquer *et al.*, 1992). Thus, the current distribution of *B. gregarius* may reflect paleogeographic movements of their teleost hosts during the last strong climatological events which have affected this geographical area (Fig. 3). This hypothesis of ancient migrations is corroborated by other data obtained on Foraminifera fossils (Thunnel & Belyea, 1982; Zachariasse & Spaak, 1983).

HOST PHYLOGENY

The close relationships which link parasites to their hosts have led several authors to consider the genealogical relationships of parasites as a source of information for the genealogical relationships of their hosts since the 19th century (von Ihering, 1891). Hennig (1966), the founder of the cladistic approach, has discussed the "parasitological method". At the beginning of their paper, Patterson, Gray & Wallis (1995) relate a colourful debate which occurred in 1957 between 2 scientists concerning the use of the systematics of parasites to comment on the phylogenetic relationships of their hosts. This reminder clearly illustrates the centre of the problem: do parasites constitute reliable informative characters to our understanding of the evolutionary relationships of their hosts? Brooks (1981a, b) was the first parasitologist to propose different coding methods in order

to use parasites as phylogenetic prints of their host systems. But, it should be pointed out that the use of parasitic information to reconstruct host phylogeny requires at least 2 conditions to be met: (i) no host switching; (ii) a real knowledge of parasite systematics and phylogeny. This is the reason why O'Grady & Deets (1987) proposed a method which considers intrinsic organic characters and parasite phylogenies together to reconstruct host phylogeny. If this kind of approach is very attractive, the few papers on this topic reflects our probably limited knowledge concerning the rates of host switching and of parasite speciation. Patterson *et al.* (1995) demonstrated cospeciation and host switching events within a host-parasite assemblage by comparing 2 phylogenies of a group of seabirds reconstructed from molecular and behavioural data on one hand, and from the systematics of their feather lice on the other hand. It is noteworthy that the only work which strongly supports cospeciation events between host and parasite lineages concerns pocket gophers and their assemblage of chewing lice (Hafner & Nadler, 1988; Hafner *et al.*, 1994). Endocellular symbionts like *Wolbachia* and *Rickettsia* which are transmitted by vertical transfer through host generations, may represent an ideal situation for parasite phylogenetic prints of hosts. Unfortunately, recent studies performed on *Wolbachia* show that they spread by horizontal transfer across host lineages as evidenced by the non-congruence of the phylogenetic relationships of

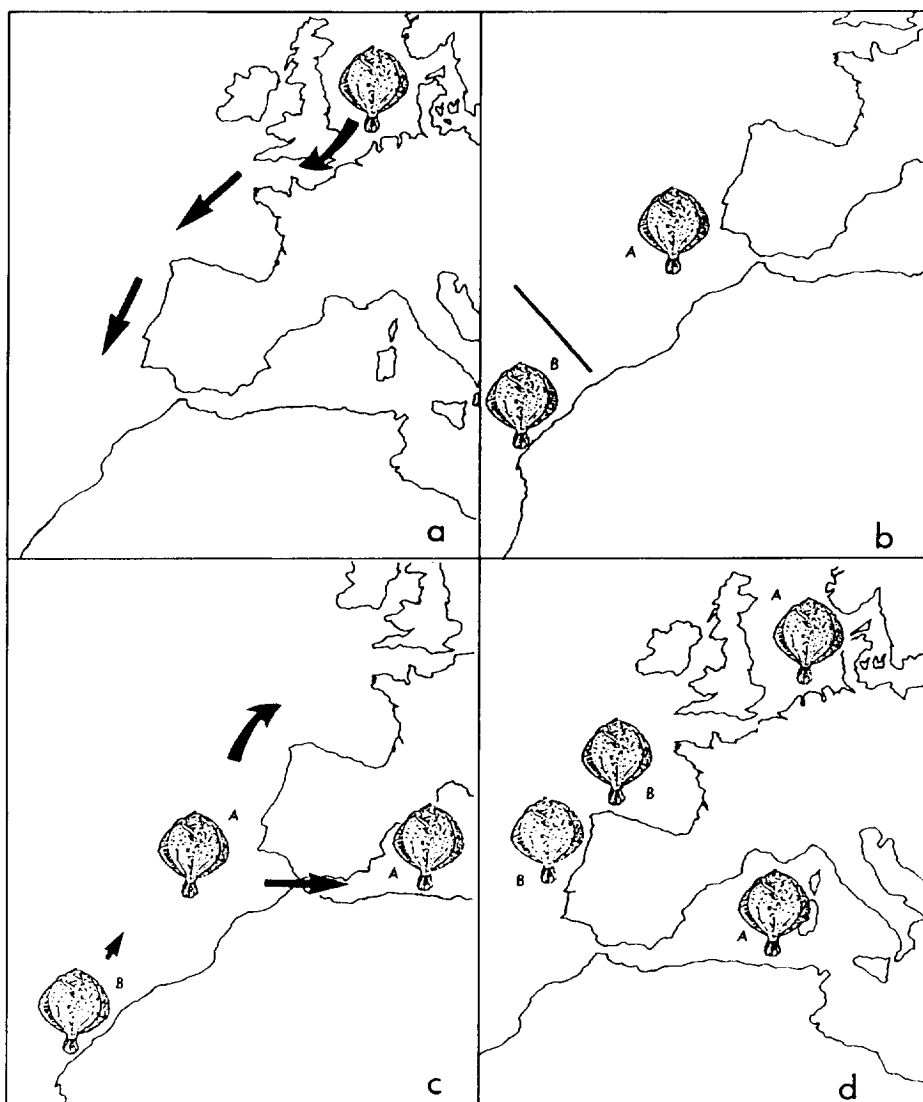


Fig. 3. Paleogeographic hypothesis of the divergence observed between the 2 genetic entities of *Bothriocephalus gregarius*. After the southward migration of the original population (a), a break in gene flow between southern and northern populations is thought to be responsible for genetic divergence (b). Following the warming of the climate, host and parasite populations recolonized their original region (c), leading to the currently observed situation (d) (see Renaud, Blanquer & Gabrion, 1990).

Wolbachia and their hosts (Rousset *et al.*, 1992). Thus, if parasites can, in theory, represent host phylogenetic prints, the significance of their contribution to the knowledge of the evolutionary history needs to be clearly demonstrated. This is becoming possible by the development of molecular tools and the emergence of new powerful statistical methodologies which will allow one to reconstruct and to test the evolutionary history of host-parasite associations (see Page, 1994).

HYBRIDIZATION AND HYBRID ZONES

Hybrids produced by the mixing of 2 parental haplotype species may constitute new environments for parasite taxa. In Lake Mikri Prespa (Northern Greece), Dupont and Crivelli (1988) made an analysis of the richness of parasite species in different cyprinid fishes. During their investigations, they found specific monogenean species which parasitized 2 fishes belonging to the genera *Alburnus* and *Rutilus*

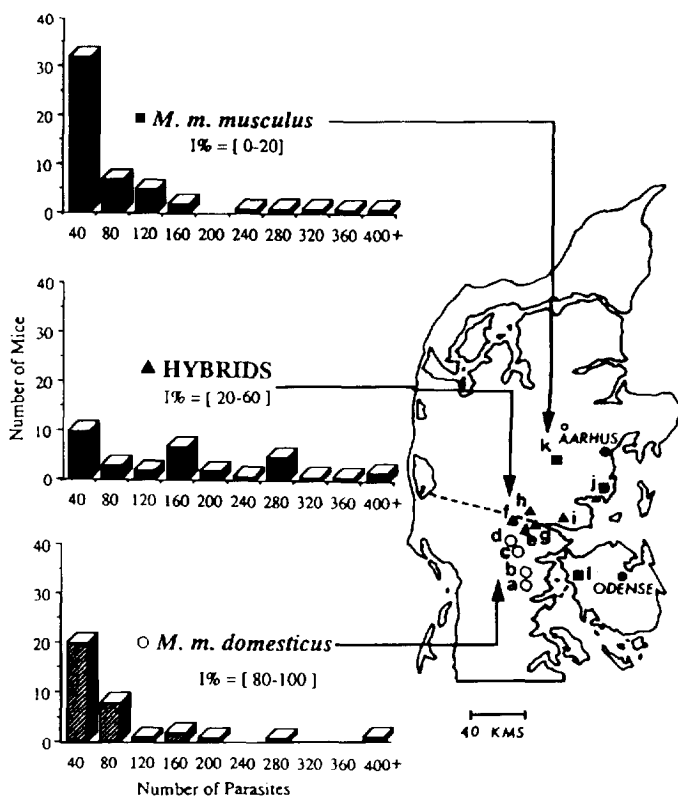


Fig. 4. Parasitism of mice by oxyurids (Nematoda) in the hybrid zone (Denmark) 1%=Hybrid index (hybridization is calculated as a measure of the introgression of the *Mus musculus musculus* genome: 100%=pure *M. m. domesticus*; 0%=pure *M. m. musculus*); a-k=sampling localities; ---=centre of the hybrid zone (see Mouliia *et al.*, 1991).

respectively. They were surprised to find several individual specimens of fish harbouring simultaneously monogeneans from the 2 fish taxa. Thus, they performed a genetic analysis on these particular specimens of fishes and found that they were all hybrids (F1) between *Alburnus* and *Rutilus*. Similar observations are reported by Cloutman (1988). This situation indicates the strict dependence which links parasites to their host, and in this context hybrid hosts represent genotypic novelties for colonization by parasites.

Results described above are based on the specificity displayed by parasites (i.e. qualitative observations), but the distribution of 1 parasite species (i.e. quantitative observations) can also provide information on the genetic status of individuals within populations. In the hybrid zone between the 2 European mice species (*Mus musculus domesticus* and *M. m. musculus*), it was demonstrated that mice with recombinant genotypes harboured significantly greater pinworm loads than mice of the parental taxa (Sage *et al.*, 1986; Mouliia *et al.*, 1991) (see Fig. 4). This

differential susceptibility of recombinant genotypes was confirmed by an experimental analysis of controlled infestation (Mouliia *et al.*, 1993). Thus, recombinations which occur in the contact zone between the 2 mice taxa can disrupt the genomic harmony (i.e. the different coadapted genetic systems in parental populations), and provoke a hybrid dysgenesis revealed by an increased susceptibility to parasitic helminths. Although the selective constraints represented by these parasites are unknown, the "super-infestation" by helminths of the hybrid genome tags the hybrid dysgenesis.

CONCLUSIONS AND PERSPECTIVES

Studies concerning parasites as host ecological tags are far more numerous than those which refer to parasites as host evolutionary prints. Why is this? Different hypotheses can be proposed: (i) there are more ecological investigators than evolutionary investigators; (ii) molecular methods which have enabled progress in the evolutionary field are

younger than ecological methods; (iii) it is more appropriate to use parasites as host ecological tags than as host evolutionary prints. Although a large disparity exists between works which refer to parasites as host tags (i.e. parasites as ecological tags vs evolutionary prints), this review demonstrates that parasites can constitute suitable evolutionary prints, but further investigations are needed. Our efforts should focus on improving current methods (i.e. genetic and molecular) and our ability to interpret the evolutionary information contained in parasitological data. Thus we propose several fields of investigation which seem important to that purpose.

The use of parasites as host evolutionary prints should be developed in the analyses of host phylogeny. Currently, the only work which compares evolutionary rates of molecular differentiation in a host-parasite association suggests that parasite genomes evolve at least 3-times faster than host genomes (Hafner *et al.*, 1994). Indeed, DNA sequences for the gene encoding mitochondrial cytochrome oxidase I in a group of rodents and their ectoparasites provide evidence for cospeciation and higher rates of nucleotide substitution in parasite lineages. Thus, if parasite genomes differentiate more rapidly than those of their hosts, we can expect that parasites could be used as evolutionary prints. However, cospeciation must be the rule in the evolutionary history of the heterospecific assemblage. Parasite phylogeny will reflect in this case the host phylogeny for which we cannot obtain enough information. Unfortunately, this field is almost unexplored since we are ignorant of most of the evolutionary histories of parasite taxa (i.e. cospeciation versus host switching). We need to understand the evolution of the parasites themselves. What are the selective pressures and constraints acting on these organisms? Information about parasite phylogeny is only beginning to be incorporated in tests of evolutionary hypotheses (Poulin, 1995a, 1995b). Development of comparative molecular analyses represents an exciting field of future research.

The choice of viable host-parasite associations to be studied needs to be considered carefully. We think that we can be ambitious at gathering new information about the major evolutionary events which have shaped the organisation of life. For example, the Polystomatidae are the only monogenean family which parasitize 2 large taxa of terrestrial vertebrates (i.e. amphibians and chelonians). Indeed, almost all other monogeneans parasitize chondrichthyan or teleost fishes. Moreover, the Polystomatidae have a wide geographical distribution including North and South America, Africa, Madagascar, Europe, Asia

and Australia. Thus, we suspect that such a group of parasites may constitute prints of major evolutionary events like the colonisation of land by vertebrates on one hand, and continental drift on the other hand. Molecular analyses are currently in progress on this group of parasites to generate information on this topic (C. Combes, personal communication). We think that the search for such host-parasite models which involve fundamental questions concerning evolutionary mechanisms represent an important aspect for the development of evolutionary parasitology as a discipline.

In this paper, we have drawn attention to the narrow relationships which link parasites to their hosts, and the potential use of this phenomenon in biosystematics. Surprisingly, knowing the high specificity of some parasite taxa (e.g. copepods, monogeneans, cestoda...), their use in host systematics is quite "underexploited". When parasitological information clearly suggests the existence of in host taxonomy, we immediately use other criteria (e.g. morphoanatomical, genetic, molecular) to define the host taxa. Unfortunately, parasites are never considered as taxonomic criteria. Parasitologists should promote this unique attribute of parasites to systematists and evolutionists.

At the infraspecific level, we should develop the use of parasites to understand different mechanisms of host evolution. We described above the case of hybrid dysgenesis suggested by the differential parasite loads harboured by host genotypes in a mice hybrid zone. In this case, parasites represent 1 biological constraint which could explain the counter selection of hybrids and the maintenance of this narrow contact zone. An opposite case suggests a phenomenon of higher resistance of host individuals to parasites which could reflect an ancient hybridization event between 2 Robertsonian mice strains in Scotland (Ressouche, personal communication). Thus, at the level of the evolutionary biology of the host population, 2 main issues can be addressed by parasitological studies: (i) qualitative and quantitative distributions of parasites between host genomes may reflect evolutionary events or mechanisms which are responsible for the structure observed; (ii) the contribution of the parasites to the function and evolution of population organisation (e.g. hybrid zones and metapopulations).

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