

Evolution and determinants of host specificity in the genus *Lamellodiscus* (Monogenea)

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The evolution and determinants of host specificity in *Lamellodiscus* species (Monogenea, Diplectanidae) were investigated. The 20 known Mediterranean species were studied, all parasites of fishes from the family Sparidae (Teleostei). An index of specificity, which takes into account the phylogenetic relationships of their fish host species, was defined. The link between specificity and its potential determinants was investigated in a phylogenetic context using the method of independent contrasts. Host specificity in *Lamellodiscus* species appeared to be highly constrained by phylogeny, but also linked to host size. Mapping specificity onto the parasite phylogenetic tree suggests that specialist species do not represent an evolutionary dead end, and that specialization is not a derived condition. It is hypothesized that the ability to be generalist or specialist in *Lamellodiscus* is controlled by intrinsic, phylogenetically-related characteristics, and that specialist species tend to use large hosts, which may be more predictable. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 431–443.

ADDITION KEYWORDS: comparative analysis – fish – parasite – phylogenetic inertia – Platyhelminthes – predictability – Sparidae – specialization.

INTRODUCTION

The mechanisms underlying specialization, the process which results in specificity (a species depending on a particular resource or set of resources), are not fully understood in ecology. Some organisms are restricted to a narrow set while others seem to be far less selective. The wider the range of niches an organism is able to exploit, the greater its evolutionary potential should, in theory, be. However, Timms & Read (1999) demonstrated that the ideal organism able to use all ecological niches does not exist; on the contrary, many very specialized organisms are found in nature. A number of studies (e.g. Fox & Morrow, 1981; Futuyma & Moreno, 1988; Wilson & Yoshimura, 1994; Fry, 1996; Gemmill, Vinet & Read, 2000) have

used theoretical models to explain the appearance of specificity. Ward (1992) suggested, using a simple mathematical model, that organisms tend to specialize on predictable resources, i.e. those that are stable through time, thus minimizing extinction risks.

Since specificity is commonly believed to be the result of an adaptive process (Brooks & McLennan, 1991; Begon, Harper & Townsend, 1996), it is important to take the phylogenetic relationships of the parasitic species being examined into account when studying its causes and evolution (Brooks & McLennan, 1991; Harvey & Pagel, 1991). This allows one to discriminate between the relative effects of past (phylogenetic) and present-day (ecological) influences (Futuyma & Moreno, 1988; Brooks & McLennan, 1991).

Host–parasite systems provide useful models for studying evolutionary problems (see Price, 1980; De Meeûs, Michalakis & Renaud, 1998; Paterson & Banks, 2001). The ecological niche of a parasite is generally easier to define than that of a free-living organ-

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ism (Timms & Read, 1999), since its main environment, habitat and food are represented, at least in part, by its host. In addition, a phylogeny of the host provides the opportunity to hypothesize about the evolution of the habitat of the parasite. Understanding the determinants of host specificity is a key issue in evolutionary parasitology (Rohde, 1994; Thompson, 1994) and essential for the control of parasitic zoonoses (Secord & Kareiva, 1996).

Following Poulin (1992, 1997), only host specificity on the part of parasites will be considered here. Host specificity is defined as the number of host species used by a given parasite species; it is the same as host range (LyMBERY, 1989). A parasite species inhabiting a single host species is usually described as a specialist (e.g. Euzet & Combes, 1980; Ludwig, 1982), whereas if it inhabits several it is said to be a generalist. It should be remembered that specificity is inversely related to host range, so that it decreases while host range increases. These concepts are relative (e.g. Kitahara & Fuji, 1994): parasite species inhabiting either a single genus or an entire family may be termed specialists (Ludwig, 1982). According to Futuyma & Moreno (1988), 'specialization must lie in the eye of the beholder'.

Parasites depend on their hosts to survive. Several hosts can be involved in a parasite's life cycle, thereby complicating the pattern of specificity and its potential determinants. Studying a parasite with a simpler life cycle avoids these difficulties. This is why a group of monogeneans was chosen for the present study. Monogeneans are almost entirely dependent upon their hosts, which constitute their sole environment throughout the life cycle, and they are known to be generally highly host-specific (Baer, 1957; Kennedy, 1975; Rohde, 1979, 1982; Noble *et al.*, 1989; Sasal, Desdevises & Morand, 1998). Barker (1991), Poulin (1992), and Kearn (1994) suggested that their high degree of host specificity might be explained by tight coevolutionary interaction with their hosts. This was also hypothesized by Tinsley & Jackson (1998) for polystomatid monogeneans found in amphibians. Humphery-Smith (1989) listed characteristics favouring host-parasite coevolution by cospeciation, with parasites highly specific and non-pathogenic to their hosts. This description matches that of monogenean parasites. However, some authors (e.g. Brooks & McLennan, 1991) believe that monogeneans possess characteristics which perfectly adapt them for surviving numerous host-switching events. This would suggest that determinants other than host evolutionary history control parasite specificity. In addition, several studies suggest that many monogeneans do not exhibit cospeciation patterns with their hosts (Klassen & Beverley-Burton, 1987, 1988; Desdevises *et al.*, 2000, in press). Sasal *et al.* (1999) have suggested that

specialist monogeneans tend to parasitize larger fish species than generalists do. This presupposes the existence of an adaptive strategy which differs from strict and passive phylogenetic tracking. As a potential factor limiting host specificity, competition does not seem to be an important determinant of specificity in monogeneans (Euzet & Combes, 1998). Indeed, most monogeneans are skin or gill ectoparasites, and they live in an environment where the number of available niches seems to be very high (Rohde, 1978). It is only when space is limited (e.g. for endoparasitic species) that competition could play a role (Jackson, Tinsley & Hinkel, 1998). This has led some authors to propose a 'mating hypothesis' to explain the high host specificity of some parasite species: in low-density populations, individuals tend to meet on a single resource to mate (Rohde, 1979; Colwell, 1986). While this hypothesis has been questioned by other authors (e.g. Adamson & Caira, 1994) it also supports the idea that there are ecological determinants for host specificity.

Futuyma & Moreno (1988) insist that the causes and consequences of specialization should not be confused, even if the distinction is not straightforward, since a single factor can be both a cause and a consequence of specificity, i.e. be the product of specificity via an adaptive process while also constraining subsequent specialization.

The host-parasite association studied here is formed by fishes from the family Sparidae (Teleostei) and their gill monogenean parasites from the genus *Lamellodiscus* Johnston & Tiegs, 1922 (Diplectanidae). This study was carried out in the north-western Mediterranean Sea near the Golfe du Lion, on all known *Lamellodiscus* species (20) in this area (see Oliver, 1987). *Furnestinia echeueis* (Wagener, 1857) is considered to belong to the *Lamellodiscus* genus (Desdevises, 2001). This host-parasite system has been widely studied, and its current pattern of host specificity can be considered to be one of the best-known in the world (Caro, Combes & Euzet, 1997). Sampling bias, if any, can be considered to be very small. Phylogenies, reconstructed from DNA sequence data, are available for both hosts and parasites (Desdevises, Morand, Jousson & Legendre, in press). A wide range of specificity can be found in this genus (from 1 to 6 hosts, see Table 1), which is relatively rare for monogeneans, and makes this host-parasite system of special interest for the study of specificity. Studying host-parasite coevolution in *Lamellodiscus*, Desdevises *et al.* (in press) suggested that the host and parasite phylogenetic trees were not generally congruent, and that almost no cospeciation seems to have occurred between these two species complexes. Therefore, choice of hosts and specialization of the parasites does not appear to be controlled by the host evolutionary history. The same authors also observed that hosts

Table 1. Data on *Lamellodiscus* species (including *Furnestinia echeneis*): parasite maximum size (in μm), host species, host maximum size (in mm), and specificity (classes). The main hosts for generalist parasites are in boldface

Parasite species	Parasite size	Host	Host size	Specificity
<i>F. echeneis</i>	1100	<i>Sparus aurata</i>	700	1
<i>L. baeri</i>	1000	<i>Pagrus pagrus</i>	750	1
<i>L. bidens</i>	1020	<i>Diplodus puntazzo</i>	600	1
<i>L. coronatus</i>	1000	<i>Diplodus annularis</i>	240	3
		<i>Diplodus cervinus</i>	550	
		<i>Diplodus sargus</i>	400	
<i>L. drummondi</i>	420	<i>Pagellus acarne</i>	360	1
<i>L. elegans</i>	520	<i>Diplodus annularis</i>	240	4
		<i>Diplodus sargus</i>	400	
		<i>Diplodus vulgaris</i>	450	
		<i>Oblada melanura</i>	300	
		<i>Spondyliosoma cantharus</i>	600	
<i>L. ergensi</i>	600	<i>Diplodus annularis</i>	240	3
		<i>Diplodus puntazzo</i>	600	
		<i>Diplodus sargus</i>	400	
		<i>Diplodus vulgaris</i>	450	
<i>L. erythrini</i>	580	<i>Pagellus erythrinus</i>	600	1
<i>L. fraternus</i>	430	<i>Diplodus annularis</i>	240	2
		<i>Diplodus vulgaris</i>	450	
<i>L. furcosus</i>	670	<i>Diplodus annularis</i>	240	3
		<i>Diplodus sargus</i>	400	
<i>L. gracilis</i>	700	<i>Diplodus annularis</i>	240	3
		<i>Diplodus sargus</i>	400	
		<i>Oblada melanura</i>	300	
<i>L. hillei</i>	1050	<i>Diplodus puntazzo</i>	600	1
<i>L. ignoratus</i>	640	<i>Diplodus annularis</i>	240	4
		<i>Diplodus puntazzo</i>	600	
		<i>Diplodus sargus</i>	400	
		<i>Diplodus vulgaris</i>	450	
		<i>Lithognathus mormyrus</i>	550	
		<i>Sarpa salpa</i>	460	
<i>L. impervius</i>	550	<i>Diplodus puntazzo</i>	600	1
<i>L. knoeffleri</i>	730	<i>Spondyliosoma cantharus</i>	600	4
		<i>Spicara maena</i>	250	
		<i>Spicara smaris</i>	200	
<i>L. mirandus</i>	800	<i>Diplodus sargus</i>	400	1
<i>L. mormyri</i>	480	<i>Lithognathus mormyrus</i>	600	1
<i>L. parisi</i>	550	<i>Sarpa salpa</i>	460	1
<i>L. verberis</i>	500	<i>Lithognathus mormyrus</i>	600	1
<i>L. virgula</i>	470	<i>Pagellus acarne</i>	360	2
		<i>Pagellus bogaraveo</i>	700	

which are related ecologically but not phylogenetically may have one or several parasite species in common, and that solitary species are less parasitized than gregarious species. This suggests that the choice of hosts and the subsequent specialization in *Lamellodiscus* monogeneans is driven by opportunities for colonization.

In this paper we investigate the evolution and deter-

minants of host specificity in *Lamellodiscus* species. There are five main lines of inquiry:

(1) Determining whether specificity is constrained by the phylogeny of the parasites. In other words, whether parasites with the same level of specificity are more closely related to each other than they are to other congeneric species. If so, support is given to the

hypothesis that host specificity in *Lamellodiscus* is controlled by its intrinsic heritable characteristics.

(2) Determining whether specificity is a derived condition (*sensu* Thompson, 1994). If so, this supports an old belief that specialization is an evolutionary 'dead end' (Huxley, 1942; Simpson, 1953; see Futuyma & Moreno, 1988).

(3) While searching for potential determinants, uncovering ecological variables that are significantly related to specificity, using comparative analysis (see Harvey & Pagel, 1991).

(4) Determining whether specificity is linked to taxonomic diversification, a hypothesis proposed in the literature (e.g. Brooks & McLennan, 1991, 1993). Specialization could promote species diversification by reducing gene flow (Futuyma & Moreno, 1988). Also, as specialists are less tolerant of host changes they are potentially more likely to be subjected to host selective pressures after a host switch or a cospeciation event (Brooks & McLennan, 1991). This would lead more frequently to parasite speciation. No such trend was observed among genera in the Diplectanidae (Desdevises, Morand & Oliver, 2001), although this hypothesis is tested again here at the species level.

(5) Looking for a correlation between host size and parasite body length. Such a link would represent a mechanism optimizing the morphological adaptation of parasites to their hosts, and would therefore be related to host specificity.

MATERIAL AND METHODS

SAMPLING

Sparid fishes and their *Lamellodiscus* parasites were sampled in several locations in the north-western Mediterranean Sea, following the protocols described in Desdevises *et al.* (2000) and Desdevises (2001). Data on *Lamellodiscus* monogeneans and their pattern of specificity were adapted from Oliver (1969a,b, 1973, 1974, 1987), Euzet & Oliver (1966, 1967), Euzet (1984), Euzet, Combes & Caro (1993), Kouider El Ouahed-Amine (1998), Desdevises *et al.* (2000) and Desdevises (2001). Parasite body lengths were measured with an optical micrometer; dimensions were comparable to those reported in the literature. Note that *L. virgula* Euzet & Oliver, 1967 and *L. obeliae* Oliver, 1973 are considered to be the same species (*L. virgula*) on the basis of molecular evidence (Desdevises *et al.*, 2000) and that *Furnestinia eche-neis* is considered to be a *Lamellodiscus* species because of its phylogenetic position (Desdevises, 2001). One of the *Lamellodiscus* species can be found parasitizing a non-sparid fish: in addition to its main host *Spondyliosoma cantharus* (Linnaeus, 1758) (Sparidae), *L. knoeppferi* Oliver, 1969 is also found

on two centracanthids, *Spicara maena* (Linnaeus, 1758) and *S. smarís* (Linnaeus, 1758).

LINK BETWEEN SPECIFICITY AND PHYLOGENY

Specificity is represented here by the number of hosts that a parasite is inhabiting (as in Poulin, 1992; see Lymbery, 1989). This can lead to classifying parasites inhabiting a single host as 'specialists', and those inhabiting two or more as 'generalists'. However, this distinction could be considered rather arbitrary. If there is no ambiguity for specialist parasites, and there is no doubt that some parasites are 'true' generalists (i.e. parasitizing several distantly related hosts across genera or families), other species parasitize several closely related hosts and could also be said to be generalists. An extreme case would be a parasite that inhabits two very closely related hosts, which could be labelled a generalist. However, it can also be argued that a classification of specificity based only on the number of hosts may lead to arbitrary distinctions between species inhabiting, for instance, five or six host species. On the other hand, a parasite species inhabiting two hosts may not be considered the same way depending on whether these two hosts are closely phylogenetically related or not.

We decided to use four semiquantitative classes to account for specificity: (1) *specialists* inhabiting a single host; (2) *intermediate specialists* inhabiting two closely related hosts; (3) *intermediate generalists* inhabiting two or more hosts in the same clade; (4) *generalists* inhabiting two or more hosts across several clades. This index is termed the Non-Specificity Index (NSI): the higher the NSI, the lower the host specificity. We are aware that NSI relies in part on arbitrary decisions (such as whether two hosts are closely related or not), but it should be borne in mind that all measures of host specificity are, at least in part, arbitrary. The definition of the four classes requires a host phylogeny on order to define the host clades. Eight clades were defined in the host phylogeny (Fig. 1A). We considered only clades from the host phylogeny which define more or less taxonomic genera, such as *Diplodus* (with the addition of *Oblada melenura*) or *Pagellus* (without *P. erythrinus*). The pattern of host-parasite association for *Lamellodiscus* species is presented in Table 1. We used host and parasite phylogenetic trees prepared from the analysis of DNA sequences by maximum likelihood via the use of Tamura-Nei 93 models of molecular evolution (Fig. 1). Partial 16S and cytochrome-b mtDNA sequences were used for the host phylogeny, and partial 18S rDNA was used for the parasite phylogeny. Details of sequencing and phylogenetic analyses are included in Desdevises *et al.* (in press). Sequence accession

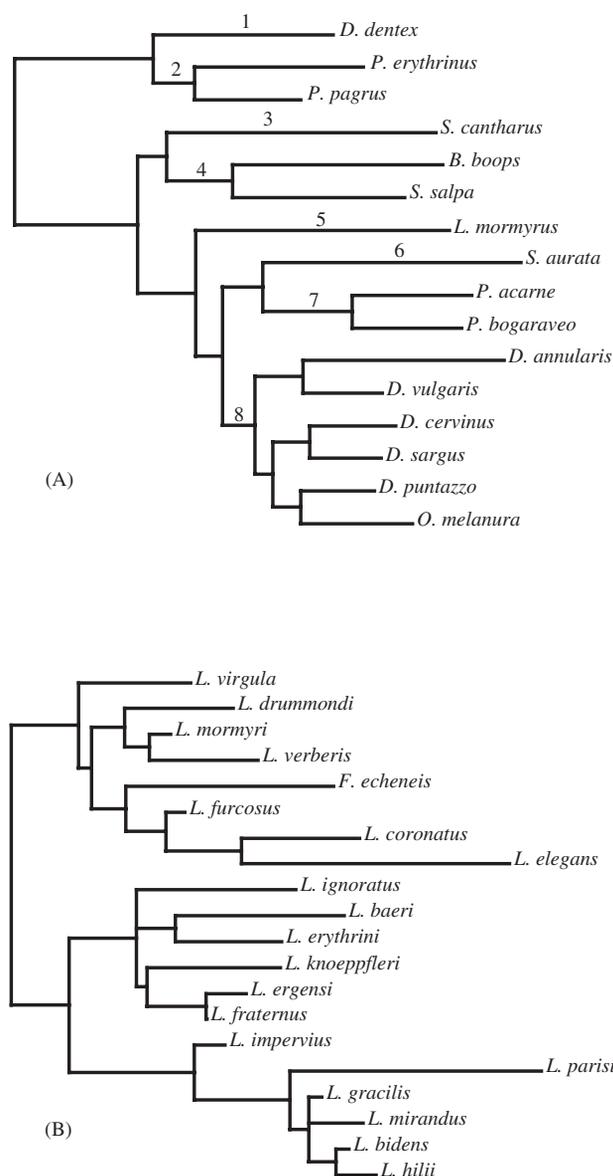


Figure 1. A, host phylogenetic tree; host clades are numbered 1 through 8. B, parasite phylogenetic tree.

numbers are available on request from the first author.

Analysis of the evolution of host specificity was carried out by parsimony character mapping (Farris, 1970; Brooks & McLennan, 1991) of NSI onto the parasite phylogenetic tree. A statistical test was also conducted using the patristic distance matrix calculated from the phylogenetic tree to assess whether NSI was significantly linked to the phylogeny. Instead of directly using the distance matrix to compare it to specificity through a Mantel test, which would require NSI to be transformed into a distance matrix, we

decided to transform instead the patristic distance matrix into principal coordinates, a technique which has been shown to be efficient at representing phylogenetic inertia (Diniz-Filho, de Sant'Ana & Bini, 1998). Vector NSI was regressed onto the resulting principal coordinates. A principal coordinate analysis (PCoA) was first performed on the phylogenetic distance matrix using R v. 4.0 (Casgrain & Legendre, 2000). Together, the computed principal coordinates (PCs) fully represented the phylogenetic variance. Since up to $(n-1)$ PCs can be computed for n species, this high number of explanatory variables does not allow one to test the significance of the partial regression coefficients. On the other hand, the PCs are linearly independent of one another by definition; they can therefore be divided into subsets before carrying out multiple regression without modifying the estimated regression coefficients. The PCs that are not significant in the subsets can be eliminated from the study. The existence of significant PCs would indicate a statistical link between specificity and phylogeny. Following this method, we performed two regression analyses, each one on half of the 18 PCs obtained. The regression parameters were tested by permutation using PERMUTE 3.4 (freeware written by P. Casgrain, available at <http://www.fas.umontreal.ca/biol/casgrain/en/labo/permute>).

IS SPECIFICITY A DERIVED CONDITION?

Character mapping was used to assess visually whether specificity is a derived condition. To investigate this point statistically, we regressed NSI against the number of nodes separating each species from the root of the tree. The higher this number, the more derived the species (i.e. the product of many prior speciation events). A simple linear regression was performed and tested by permutation using PERMUTE.

DETERMINANTS OF SPECIFICITY

We used the method of independent contrasts (Felsenstein, 1985), which takes phylogeny into account, to investigate the determinants of specificity. This consists of estimating the differences (contrasts) between sister taxa and implementing statistical tests using phylogenetically independent values. Contrasts must be standardized across the phylogenetic tree (Felsenstein, 1985), and the regression forced through the origin (Garland, Harvey & Ives, 1992). CAIC 2.6.7b (Purvis & Rambault, 1995) was used to compute the contrasts for NSI and the explanatory variables (below). We tried to find which variables were statistically linked to NSI via multiple regression forced through the origin using independent contrasts. The environmental variables chosen were:

(i) Maximum host size (from Whitehead *et al.*, 1986).
 (ii) Host abundance (from Whitehead *et al.*, 1986) in three semiquantitative classes: (1) rare, (2) intermediate and (3) common.

(iii) Host social behaviour (binary variable: gregarious or solitary, data from Whitehead *et al.*, 1986 and Caro *et al.*, 1997).

(iv) Number of potential hosts (Poulin, 1992), defined as the total number of species in the host clade(s) containing the parasitized host(s). For example, a parasite species inhabiting only *Diplodus sargus* possesses six potential host species, because the *Diplodus* clade contains six species (five *Diplodus* species and *Oblada melanura*, see clade 8 in Fig. 1A).

Variables (i)–(iii) were considered to be linked to host predictability (see Winemiller & Rose, 1992). As in Poulin (1992), this variable was chosen because it can be presupposed that closely related hosts will share genetic and physiological characteristics allowing their colonization by the same parasite species. Poulin found a significant relationship between host specificity and the number of potential hosts for some monogonean families.

All variables were ln-transformed in order to obtain linearization and normality of contrasts (Kolmogorov–Smirnov, $\alpha = 5\%$). Normality tests were performed using R v. 4.0.

In addition, the estimation of phylogenetic inertia by PCoA allowed the partitioning of the respective influences of phylogeny and environmental variables on the variation of specificity. These may not be independent and may act simultaneously on the response variable (Fig. 2; see Westoby, Leishmann & Lord, 1995). What we sought to identify was the proportion of variance containing a phylogenetic effect related to ecology – what Harvey & Pagel (1991) termed “phylogenetic niche conservatism”. This includes the shared attributes that related species may have acquired because they have tended to occupy similar niches during evolutionary history. Three multiple regressions were performed:

- (1) NSI on the significant PCs (calculated above).
- (2) NSI on the important environmental variables, selected via a backward elimination procedure.
- (3) NSI on the significant PCs and selected environmental variables, without using any further selection procedure.

The coefficient of determination (R^2) was calculated for each multiple regression. This allowed us to partition the variation of NSI between the environmental and phylogenetic components (Fig. 2). Fraction [a] is the purely environmental component, [c] the purely phylogenetic component, while [b] represents the variation explained by the common part of phylogeny and

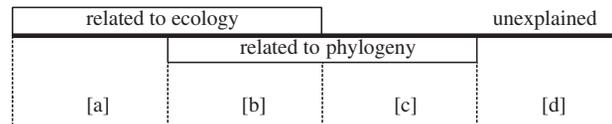


Figure 2. Variation partitioning of phylogenetic and ecological influences, for a dependent variable represented by the thick horizontal line.

environment (Harvey & Pagel’s phylogenetic niche conservatism). R^2 computed following the three regressions was as follows: (1) equal to [a + b], (2) equal to [b + c], and (3) equal to [a + b + c]; [a], [b] and [c] are then easily found by subtraction.

IS SPECIFICITY CORRELATED TO TAXONOMIC DIVERSIFICATION?

To establish whether or not NSI is linked to taxonomic diversification, we used MacroCAIC 0.8.2 (free-ware written by P.-M. Agapow, available at <http://www.bio.ic.ac.uk/evolve/software/macrocaic/>), which has been specifically devised to find such a correlation (see Desdevises, Morand & Oliver, 2001). MacroCAIC allows one to use species richness as a variable in a comparative analysis to estimate whether traits (such as host specificity in the present study) are associated with high speciation rates represented by clade species richness. Comparison of species richness is made between sister-clades at each node of the phylogeny. Barraclough, Vogler & Harvey (1998) considered this approach to be the best for studying the potential causes of taxonomic diversification. Species richness cannot be used in the same way as any other continuous variable, i.e. through independent contrasts, because, its estimated value at the nodes of the phylogeny is not the average of the values in lower phylogenetic positions, but their sum. No contrasts were calculated for polytomies. Linear regressions were assessed by testing the Pearson correlation coefficient. The variable representing species richness is the natural log (ln) of the clade ratio – the ratio, for each node of the phylogeny, of the number of species in one sister clade where the estimated value of specificity (at the node) is lowest, to the number of species in the other. When this ratio is less than 1 (negative ln), the clade with the lowest NSI contains more species; when it is equal to 1 (null ln), the number of species in each sister clade is the same; and when it is greater than 1 (positive ln), the clade with more species has the lowest specificity (highest NSI). The analysis is performed between sister clades at each node of the phylogeny. Clade ratios were regressed against standardized contrasts for ln(NSI). If the null hypothesis is false, we should observe a significantly increased diversification.

tion with specificity, which in turn produces a negative relationship with NSI.

IS SPECIFICITY LINKED TO MORPHOLOGICAL ADAPTATION?

We looked for a link between parasite body length and host size. A positive relationship may reflect the need to develop larger attachment organs to larger hosts in order to remain attached (see Sasal *et al.*, 1999). When testing for this, we assessed specialists and generalists separately. We did not use the previously defined classes of specificity (NSI) because the small number of parasites in three of the classes (except the specialists) would have produced weak statistical correlations. For generalists, several hosts are involved; to use the mean of all host sizes could bias the analysis since certain host species are much more parasitized than others. Instead, we used the size of the main host species (Table 1) where the recorded parasite abundance is greatest. When there were several main host species, the mean size was used. Simple linear regressions were computed on independent contrasts to control for phylogenetic effects. We used maximum sizes

for hosts and parasites. Host sizes were taken from Whitehead *et al.* (1986).

RESULTS

IS SPECIFICITY A DERIVED CONDITION?

Mapping specificity onto the parasite phylogenetic tree (Fig. 3) does not indicate that there are more specialists among the 'derived' than the 'primitive' species (terms which in this context refer to the particular phylogeny being discussed). As shown in Figure 3, the ancestral state in *Lamellodiscus* appears to be specialist. No statistical link can be found between NSI and the number of nodes separating the species from the root of the tree (Fig. 4, $r = 0.06$, $P = 0.800$). These results support the hypothesis that host specificity in *Lamellodiscus* is not a derived condition.

LINK BETWEEN SPECIFICITY AND PHYLOGENY

Multiple regression of NSI against the PCs extracted from the phylogenetic distance matrix found PC1, PC2 and PC5 to be highly correlated to specificity ($P = 0.001$); PCs are presented in order of decreasing

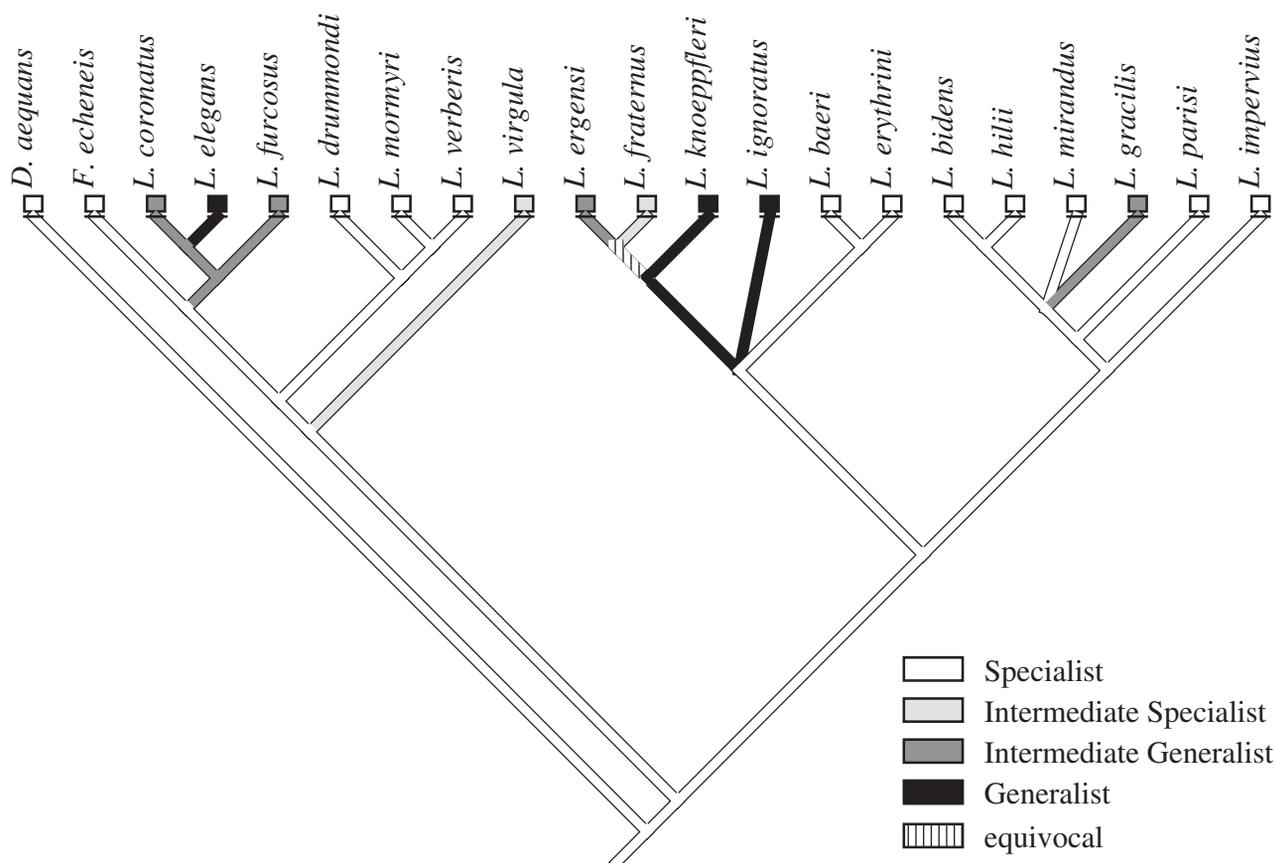


Figure 3. Mapping of specificity (NSI, 4 classes) on to the parasite phylogenetic tree.

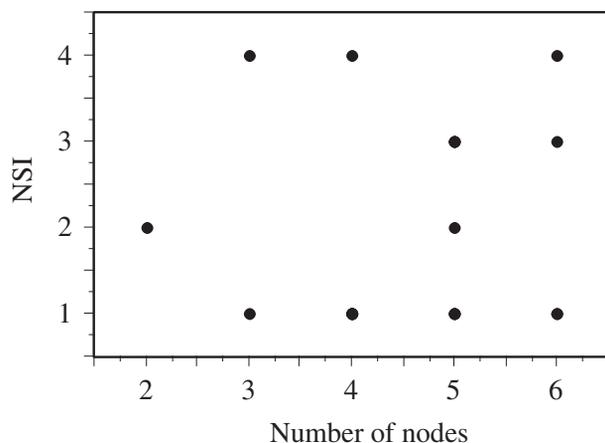


Figure 4. Dispersion diagram of host specificity against the number of nodes from the root of the tree for each species.

eigenvalues, i.e. in order of the amount of variance of the phylogeny that they represent. These three PCs account for 50.4% of the phylogenetic variance and 72.6% of the variation of NSI ($R^2 = 0.726$). This suggests that specificity is linked to phylogeny, i.e. that specialists as well as generalists tend to be grouped in the same clades. This can also be observed in the character mapping (Fig. 3).

DETERMINANTS OF SPECIFICITY

Only host size was retained by a backward elimination procedure after multiple regression of NSI on the environmental variables using independent contrasts ($r = -0.631$, $P = 0.005$). The simple linear regression of NSI on host size, after removal of the non-significant environmental variables, is shown in Figure 5. This result suggests that specialists are found on larger hosts.

The variation partitioning results (Fig. 6) are striking. As in the analysis of contrasts, host size was the only environmental variable linked to specificity; however, fraction [a], the purely environmental component, accounted for only 4% of the variation in host specificity, while [c], the purely phylogenetic component (from PCs 1, 3 and 5) accounted for 45%, and the fraction common to host size and phylogeny ('phylogenetic niche conservatism') for 24%.

IS SPECIFICITY CORRELATED TO TAXONOMIC DIVERSIFICATION?

Even if 8 out of 10 contrasts are positive, the simple linear regression of $\ln(\text{clade ratio})$ on $\ln(\text{NSI})$ suggests that specificity is not linked to taxonomic diversification in *Lamellodiscus* (Fig 7; $r = 0.331$, $P = 0.320$). To

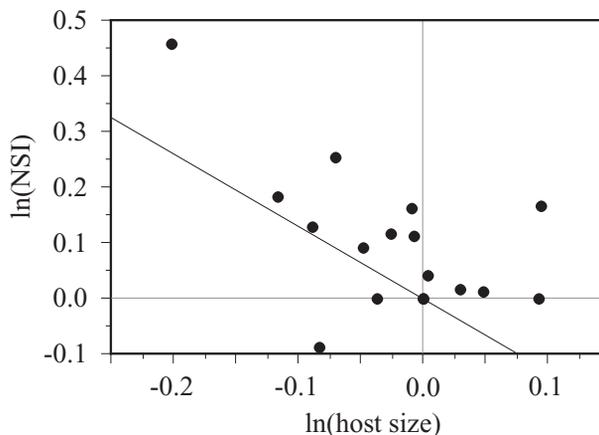


Figure 5. Simple regression of independent contrasts on host size (selected by a backward elimination procedure) against specificity.

a	b	c	d
4%	24%	45%	27%

Figure 6. Variation partitioning of host specificity by host size and phylogenetic constraints (PCs1, 2 and 5): [a] variation of host specificity due to host size alone; [b] variation due to the common influence of host size and phylogeny; [c] variation strictly due to phylogeny; and [d] the unexplained part of the variation.

have a low or high mean host specificity, a clade does not have to contain more or fewer species. However, this non-significant result may be due to a lack of power as only 10 contrasts were computed in this analysis.

IS SPECIFICITY LINKED TO MORPHOLOGICAL ADAPTATION?

We found a significant positive correlation between parasite body length and host size in all species (Fig. 8; $r = 0.719$, $P < 0.001$), specialist ($r = 0.644$, $P = 0.030$) as well as generalist ($r = 0.841$, $P = 0.004$). Similar results were observed without controlling for the phylogeny.

DISCUSSION

Our results show that host specificity in *Lamellodiscus* monogeneans is linked to host size. Specialist *Lamellodiscus* tend to use larger hosts than generalist species. The same kind of relationship was found by Sasal & Morand (1998), Sasal *et al.* (1999) and

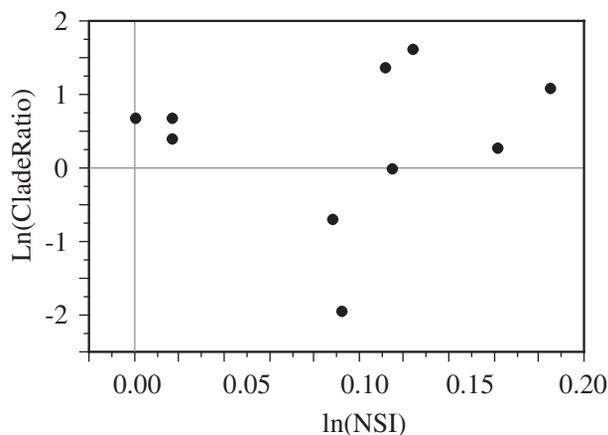


Figure 7. Dispersion diagram of independent contrasts of $\ln(\text{clade ratio})$ against host size.

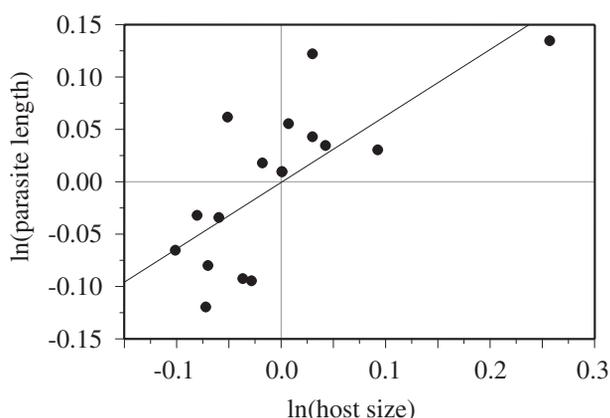


Figure 8. Simple linear regression of independent contrasts of parasite body length against host size.

Simková *et al.* (2001) for other host–monogenean systems. Since larger fish live longer and are usually found closer to the top of the food chain (Winfield & Nelson, 1991; Winemiller & Rose, 1992), they can be thought of as being more predictable, supporting the hypothesis that specialization occurred on a predictable resource (Ward, 1992). However, host size is also generally negatively linked with host abundance, another measure of predictability; it is therefore difficult to be certain that large hosts are selected by specialist *Lamellodiscus* species for this reason alone. Large fish may contain more available niches for parasite specialization than smaller fish (Dogiel, Petrushevsky & Polyanski, 1961; Kuris, Blaustein & Alio, 1980). In any case, there is no evidence of interspecific competition in monogeneans (Rohde, 1979, 1994; Simková *et al.*, 2000). Large hosts may also be considered as more easily attainable targets for larval

monogeneans, and thus decrease the cost of specialization (Morand *et al.*, 2002). Host abundance could also be seen as an indication of predictability, but it is not statistically linked to specificity. Perhaps this characteristic is more labile in evolutionary time than size, or the semiquantitative variable used to account for abundance has resulted in a decrease of statistical power, leading to a non-significant relationship. Norton & Carpenter (1998) pointed out that more generalists are present when the hosts are unpredictable, and that the key to host specificity is relative host abundance. They suggest that a threshold in relative host abundance may explain the appearance of specificity in parasites. Below it, generalism is favoured because the relative abundance of one host species is too low to maintain a parasite population. The value of this hypothetical threshold – which may have been reached in our case – may determine whether host abundance plays a role in the specificity of the parasite. The impact of relative host abundance on specificity should also be linked to parasite dispersal abilities (see Reed & Hafner, 1997) and taken into account in the assessment of the threshold. The number of potential host species is not linked to specificity, contrary to the observation of Poulin (1992), for *Gyrodactylus* monogeneans from Canada. However, the absence of phylogeny did not allow Poulin to control his results for that influence, which may explain the discrepancies of his results with ours. The colonization strategy of *Gyrodactylus* species may also be different to that of *Lamellodiscus*. Our result does not imply that the most suitable hosts (if phylogenetically related hosts are considered in this way) are not more heavily colonized by the same *Lamellodiscus* species but that if this colonization is followed by speciation for *Lamellodiscus* species, no decrease of specificity will result. It is also possible that the potential hosts should be more broadly defined, and not only by phylogenetic proximity; however, this would require thorough physiological and ecological studies.

Links between specificity and ecological factors have been encountered in other host–parasite associations. For a plant–phytophagous insect association, Smiley (1978) suggested that the appearance of specialization is due more to ecological factors (such as predation or host abundance) than to genetically controlled compatibility with the host. The appearance of biochemical or metabolic adaptations only comes after this specialization, and it prevents the possibility of colonizing other plant species. This implies that this type of compatibility is only one of the factors involved.

We did not find an increase in specificity for derived species. This has also been reported by Thompson (1994) in a review of many studies and supports the hypothesis that specificity is not an evolutionary dead-

end, as proposed by Simpson (1953), and that “there is no intrinsic direction to the evolution of specialization” (Thompson, 1994). A hypothetical specialist ancestral state followed by the appearance of generalism seems to indicate that specialization is not an irreversible condition.

The significant link between specificity and phylogeny suggests that host specificity is influenced by historically constrained characteristics. Therefore, only those groups of *Lamellodiscus* species that are phylogenetically related may be able to develop a specialist or generalist behaviour. The existence of such phylogenetic constraints is in accordance with what can be observed at a deeper taxonomic level (e.g. between classes or phyla) where some groups, like the monogeneans, show marked preferences for a type of host specificity (Sasal *et al.*, 1998). This suggests the appearance of a feature in an ancestral species constraining its descendants within a type of specificity. This hypothetical feature may not be the same in all clades. Specificity in *Lamellodiscus* monogeneans seems therefore to be determined by a mixture of historical and ecological influences. The variation partitioning results suggest that an important fraction of specificity is controlled by host size and phylogeny. It would therefore appear that related parasites tend to specialize on large hosts, and that some *Lamellodiscus* species acquired through their phylogeny the ability to be generalists (which seems to be the derived state in this genus) and thus able to use more hosts – and not only the largest species. This ability could be related to morphological, physiological or immunological factors.

The absence of a link between specificity and taxonomic diversification for *Lamellodiscus* species was previously found at a deeper taxonomic level, for the Diplectanidae (Desdevises *et al.*, 2001). This could be explained by the absence of a higher speciation or extinction rate among the specialist species (see Slowinski & Guyer, 1993). The single host on which a specialist species relies may increase the risk of extinction, even if its larger size makes it more predictable. It might also be due to insufficient statistical data – only 10 contrasts were used in the analysis, because of the relatively small number of species considered and the presence of polytomies in the phylogenetic tree. However, even when using a fully resolved tree (data not shown), there is no statistical link between specificity and diversification. Moreover, the trend observed, even if not significant, would favour the inverse hypothesis, that of an increase in the number of host species with taxonomic diversification.

The significant correlation between parasite body length (PBL) and host size (HS) suggests the existence of selective pressures exerted by the hosts on the parasites (Poulin, 1996). The fact that this link was

found with or without controlling for phylogeny also indicates an absence of strong historical constraints on PBL, therefore suggesting an adaptive nature for *Lamellodiscus* body length. In other studies, PBL has been found to be positively correlated to HS, mostly in a context of high host specificity (Morand *et al.*, 1996). For endoparasitic species, Morand & Sorci (1998) hypothesized (supported by a comparative analysis), that PBL can be related to host longevity, which is in turn correlated to HS. Long-lived hosts would provide more energy and would harbour more long-lived parasites, and consequently larger parasite species (Morand *et al.*, 1996; Morand, 1996). However, in the monopisthocotylean monogeneans, the small size (relative to the host), the probable absence of competition, and the short generation time (Rohde, 1982) suggest that resources are not a limiting factor. Morphological adaptation to the host, perhaps for stronger attachment (see Sasal *et al.*, 1999), is a more plausible explanation. Simková *et al.* (2001) observed that specialist dactylogyrid monogeneans seem to be more closely adapted to their hosts than generalists, highlighting the influence of adaptive processes for attachment to the host. This leads to the question: do *Lamellodiscus* parasites inhabit hosts for which their size is compatible, or is their size modified by the hosts they use the most for some other reason? This highlights the difficulty of disentangling causes and consequences, as pointed out by Futuyma & Moreno (1988). These authors argued that morphological and physiological adaptations may be seen to be the consequences rather than the causes of specialization, and that the determinants of specificity may be more behavioural. The fact that generalist *Lamellodiscus* species inhabit hosts with a wide range of sizes and that this relationship is significant if only the size of the main host is taken into account, suggest that this correlation is more likely to be a consequence than a cause of host specificity. This is also supported by the absence of a link between PBL and phylogeny, which would be expected if such a link existed, because specificity is significantly linked to host size. Tompkins & Clayton (1999) suggested that size is a determinant of host specificity of lice parasitizing swiftlets. The same kind of relationship has been suggested by Reed & Hafner (1997) and supported by Morand *et al.* (2000) for pocket gophers and their chewing lice. In the case of gophers, there is a match between the size of the parasite's attachment organ and the host's hair size.

Experimental studies (e.g. Gemmill *et al.*, 2000) can help provide insights into the intrinsic factors limiting the colonization of new hosts by *Lamellodiscus* parasites. The question remains: are these more likely to be causes or consequences of host specificity? Such morphological adaptations would intuitively limit

wider dispersal of specialist species; even if they were caused by an adaptive process, they would also be a determinant of specificity for the descendant species. Further study of the polymorphism and genetic variability of attachment organs is required in order to improve our understanding of this mechanism. The genetic variability of hosts should also be taken into account (Secord & Kareiva, 1996). The variation of these components of host–parasite interaction may be important factors determining the potential for colonization.

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