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Determinants of parasite species richness on small taxonomical and geographical scales: *Lamellodiscus* monogeneans of northwestern Mediterranean sparid fish

Y. Desdevises*

Université Pierre et Marie Curie (Paris VI), UMR 7628, Laboratoire Arago,
BP 44, F-66651 Banyuls-sur-Mer Cedex, France

Abstract

Determinants of parasite species richness have been investigated in a host–parasite system comprising fish of the family Sparidae and their monogenean gill ectoparasites of the genus *Lamellodiscus*. This study was carried out on a small geographical scale in the northwestern Mediterranean Sea. Host phylogenetic relationships were taken into account by phylogenetic eigenvector regression which required the reconstruction of a phylogenetic tree for the sparid fish species using mtDNA sequences. Several ecological variables potentially acting on *Lamellodiscus* species richness were considered. Host body size and host migratory behaviour appeared to be the main determinants of parasite species richness in this system. It is concluded that structuring of monogenean communities is controlled more by ecological than evolutionary factors.

Introduction

Factors linked with parasite species richness in various types of hosts have been widely investigated (e.g. Esch *et al.*, 1990; Gregory, 1990; Gregory *et al.*, 1991; Poulin, 1991a,b, 1995; Guégan *et al.*, 1992; Ranta, 1992; Morand & Poulin, 1998; Poulin & Morand, 1999; Morand & Harvey, 2000; Morand *et al.*, 2000). These studies identified various factors potentially controlling the number of parasite species in a group of hosts, such as body size (Bell & Burt, 1991; Guégan *et al.*, 1992), host distribution range (Gregory, 1990; Bell & Burt, 1991; Ranta, 1992), geographical distance (Poulin & Morand, 1999), host diet (Bell & Burt, 1991; Morand *et al.*, 2000), host density (Morand & Poulin, 1998, Morand *et al.*, 2000), host longevity (Bell & Burt, 1991; Morand & Harvey, 2000), and group-living (Poulin, 1991a; Ranta, 1992).

These studies, however, considered the total number of parasite species per host in accounting for species richness. These parasite species belong to various taxonomic groups, with different biological characteristics such as the complexity of life cycle and transmission mode. Therefore, these different types of parasites may be subjected to different factors potentially influencing their species richness. For example, richness in digeneans could be controlled by host diet because infective stages are transmitted via food ingestion, whereas monogeneans have no reason to be controlled by such an influence. On the contrary, ectoparasites such as lice, monogeneans, or copepods may be transmitted via direct host contact and thus host social behaviour plays more of a role in species composition than for endoparasites like acanthocephalans, digeneans, or nematodes. Thus, in studies considering species richness as the total number of parasite species, the hypothetical variables linked to richness act differently on the various components of the parasite community. Some factors can even inversely influence a parasite group relatively to another. For example, anadromous fish species, when they leave freshwater for saltwater, can lose their ectoparasites while retaining their endoparasites and even acquiring new species. The richness of ectoparasites may then decrease while endoparasite species richness increases under the influence of the same factor. This example also reveals the importance of geographical scale in a study on species richness: in this case, the total number of parasite species differs if one or both environments are considered. The number of parasite species can indeed vary within the

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*Fax: (33) (0)4 68 88 16 99;
E-mail: desdevises@obs-banyuls.fr

host's geographical range (Gregory, 1990). This range can therefore be controlled, either by considering it as a variable in the analysis or by carrying out the study in a given geographical area. In addition, through processes of host–parasite coevolution (Brooks & McLennan, 1991; Page & Charleston, 1998), parasite species richness could be influenced by host phylogeny (Poulin, 1995; Morand & Poulin, 1998), and host taxa cannot be considered as independent points. It is then essential to control for phylogenetic effects with an appropriate method in such comparative analyses (see Harvey & Pagel, 1991; Martins *et al.*, 2002).

To control for this multiplicity of effects, the present study was carried out on a small taxonomical and geographical scale, by investigating the determinants of the number of parasite species from a given genus in host species belonging to a single marine fish family. This study focuses on those factors controlling species richness of monogeneans from the genus *Lamellodiscus*, which includes gill parasites of fish from the family Sparidae in the northwestern Mediterranean Sea.

Materials and methods

Sampling of hosts and parasites

In the northwestern Mediterranean Sea, 14 species of sparid fish are parasitized by monogeneans belonging to the genus *Lamellodiscus* (Euzet *et al.*, 1993). In the study area, this host–parasite association has been thoroughly studied (Euzet & Oliver, 1966, 1967; Oliver, 1969a,b, 1973, 1974; Euzet, 1984; Euzet *et al.*, 1993; Desdevises *et al.*, 2000, 2002a,b; Desdevises, 2001) and can be considered as well known over a long time. In particular, sampling error can be considered as small, if any. In the present study, *Lamellodiscus virgula* and *L. obeliae* are considered to be the same species (*L. virgula*) on the basis of molecular evidence (Desdevises *et al.*, 2000), and *Furnestinia echeneis* is considered to be a *Lamellodiscus* species because of its phylogenetic position within the *Lamellodiscus* genus (Desdevises, 2001). Monogeneans possess a direct life cycle and infect their hosts via a free-swimming larval stage, the oncomiracidium (see Schmidt & Roberts, 1989). However, transmission of adult parasites via host contact has been hypothesized (Bakke *et al.*, 1992). Sparid fish were caught in the Golfe du Lion near Banyuls-sur-Mer, France. *Lamellodiscus* monogeneans were dislodged from fish gills under a dissecting microscope and identified using morphological characteristics of the haptor and copulatory organ. Richness in *Lamellodiscus* species is expressed as the number of parasite species recorded per host species in the study area, and compared with that in the literature.

Phylogeny

Hanel & Sturmbauer (2000) reconstructed a phylogenetic tree of sparid fish based on 16S mtDNA, for 24 species from the Atlantic Ocean and the Mediterranean Sea (including the 14 Mediterranean species under study here, see Whitehead *et al.*, 1986), although their tree showed considerable differences from the current taxonomy. To infer the phylogenetic relationships among sparids and to perform an independent external validation of the Hanel & Sturmbauer dataset, cytochrome-b mtDNA as described by Jousson *et al.* (2000) and Desdevises *et al.* (2002a) was used to reconstruct different phylogenetic trees. DNA extraction and sequencing followed the same protocol as in Desdevises *et al.* (2000). Sequence data are available in the GenBank™, EMBL and DDBJ databases under the accession numbers AJ247269, AJ247277, AJ247279–AJ247281, AJ247283–AJ247286, AJ247290, AJ247291, AJ247293, AJ247294, AJ247296, AJ276879–AJ276881, AJ277366–AJ277371, AJ319809, AJ319811–AJ319813. These sequences were used along with the 16S mtDNA in a 'total evidence' approach (see Lapointe, 1998) after verifying the homogeneity of the dataset via a partition homogeneity test (Farris *et al.*, 1994). *Gadus morhua* (GenBank accession number: NC002081, complete mitochondrial DNA) was used as an outgroup. Sequences were aligned with ClustalX (Thompson *et al.*, 1997) and visually checked. Gaps were treated as missing data. Host phylogeny was estimated via maximum likelihood (ML), using the best model chosen via a hierarchical likelihood ratio test computed by Modeltest (Posada & Crandall, 1998). Phylogenetic analyses were performed with PAUP* 4.0b10 (Swofford, 2002) with a heuristic search algorithm, the tree-bisection-reconnection branch swapping option, and a random addition sequence (10 replicates). The tree was validated with a bootstrap procedure (1000 replicates), but because the use of ML was computationally too intensive for this analysis, the neighbour-joining method (Saitou & Nei, 1987) was used with distances corrected by the same model as that for the ML reconstruction, as well as a maximum parsimony analysis conducted with the heuristic search algorithm of PAUP* 4.0.

Comparative analysis

Several variables were chosen as potential determinants of monogenean species richness, and were taken from the literature (Whitehead *et al.*, 1986; Caro *et al.*, 1997). These variables are related to host biology and ecology (table 1), and are:

1. Body size. This can relate to the number of available niches for parasite species (see Guégan *et al.*, 1992; Rhode, 1994), and then directly influence parasite species richness, including monogeneans.
2. Abundance. A greater number of available host individuals can more easily sustain populations of their parasite species (Bell & Burt, 1991), therefore increasing species richness.
3. Displacement (sedentary or migratory behaviour). Sedentary hosts can support more easily local parasite species. Conversely, hosts undergoing migration may encounter more parasite species and therefore increase their richness (Gregory, 1990).
4. Social behaviour (gregarious or solitary). Some monogeneans are believed to be transmitted via host contact (see Bakke *et al.*, 1992), in addition to the usual larval infections. Gregarious hosts may also represent larger targets for monogenean species

Table 1. Richness of *Lamellodiscus* species on northern Mediterranean sparid fish species relative to host size, abundance, displacements and social behaviour.

Sparidae	Richness	Size	Abundance	Displacements	Social behaviour	Sample size	Number of studies
Diplodus annularis	7	24	1	1	1	≥65	3
Diplodus cervinus	1	55	0	0	0	9	2
Diplodus puntazzo	5	60	2	1	1	≥10	3
Diplodus sargus	7	40	2	1	1	58	2
Diplodus vulgaris	6	45	2	1	1	21	2
Lithognathus mormyrus	2	55	2	0	0	≥17	4
Oblada melanura	2	30	2	0	1	20	2
Pagellus acarne	2	36	2	0	1	63	4
Pagellus bogaraveo	1	70	2	0	1	23	4
Pagellus erythrinus	1	60	2	0	1	29	3
Pagrus pagrus	1	75	1	0	0	≥10	3
Sparus aurata	1	70	2	1	0	≥8	4
Spondyliosoma cantharus	2	60	1	0	1	≥8	2
Sarpa salpa	2	46	2	0	1	≥26	3

Size: maximum body size in cm; abundance: 0 = rare, 1 = intermediate, 2 = common; displacements: 0 = sedentary, 1 = migratory; social behaviour: 0 = solitary; 1 = gregarious; sample size: total number of fish examined per species in the study area from the surveyed literature (cited in text) and the present study (≥ indicates that some references do not mention sample size and are thus considered equal to 1); number of studies: number of publications where fish species are examined for *Lamellodiscus* species in the study area (when the same fish sample is used in several studies, only 1 is counted).

(see Morand *et al.*, 2002), therefore increasing their probability of colonization and then monogenean species richness.

The most widely used approach for comparative analysis is the independent contrasts method (Felsenstein, 1985). However, this technique is designed for studying continuous variables, which is not the case here for several variables. Another method designed by Diniz-Filho *et al.* (1998), the phylogenetic eigenvector regression (PVR) was therefore chosen. This method expresses phylogenetic variance among species via principal coordinates (PCo) computed from the patristic distance matrix derived from the species phylogenetic tree. The PCo are found via a principal coordinate analysis (see Legendre & Legendre, 1998), and are then used in a multiple regression to represent the phylogenetic variance, along with the ecological variables. The high number of PCo obtained (up to $n - 1$ for n species in the phylogenetic tree) leads to overparameterization of the model, especially when the ecological variables are added. This is the reason why some PCo must be selected to represent the phylogenetic variance. Diniz-Filho *et al.* (1998) proposed to select PCo via a broken-stick model (see Legendre & Legendre, 1998). This technique was used here.

A multiple regression was then performed with *Lamellodiscus* species richness as the dependent variable, and ecological variables (body size, abundance, displacement and social behaviour) and selected PCo representing phylogenetic inertia as independent variables. Categorical variables were coded as dummy variables. Significant variables were selected through a backward elimination procedure (see Legendre & Legendre, 1998). This analysis was carried out using the software Permute! 3.4 (freeware written by P. Casgrain, available at URL http//www.fas.umontreal.ca/BIOL/Casgrain/en/labo/permute), which tests parameter significance via a permutational procedure (999 permutations were used here). This makes data transformation and tests of residuals for normality unnecessary.

Results

Phylogeny

The best evolutionary model for the data chosen by Modeltest was a Tamura-Nei model with a gamma distribution rate accounting for base substitution heterogeneity and a proportion of invariant sites (see parameter values in table 2). The ML phylogenetic tree for the sparid

Table 2. Parameters used in the evolutionary model in the maximum likelihood (ML) analysis for sparid phylogenetic reconstruction.

Base frequencies				Substitution rates							
A	C	G	T	A-C	A-G	A-T	C-G	C-T	G-T	Inv	α
0.277	0.296	0.146	0.282	1	9.32	1	1	13.17	1	0.504	0.589

Inv is the proportion of invariant sites; α is the shape of the Γ distribution accounting for substitution rate heterogeneity.

fish species under consideration, including bootstrap support values, is shown in fig. 1.

Comparative analysis

Only the first PCo (PCo1, representing 50.96% of phylogenetic variance) was selected via the broken-stick model, and was then kept in the analysis to represent phylogenetic inertia. The results are similar if more PCo are used to account for phylogenetic variance. Table 3 presents variable selection steps generated by the backward elimination procedure. Only the variables body size and displacement were retained in the model. *Lamellodiscus* species richness does not seem to exhibit any phylogenetic inertia, as no statistical relationship with PCo was found.

Discussion

As noted elsewhere (Hanel & Sturmbauer, 2000; Desdevises *et al.*, 2002a; Orrell & Carpenter, 2004), the phylogenetic tree obtained from molecular data for sparid fish challenges the established taxonomy (Whitehead *et al.*, 1986; Fiedler, 1991): *Oblada melanura* is nested within the *Diplodus* genus, and the genus *Pagellus* appears to be polyphyletic, with *Pagellus erythrinus* being the sister species of *Pagrus pagrus*. These latter clades are well supported by bootstrap analysis, even if higher nodes are far less robust. Discrepancies between this tree and previously published trees based on molecular data (Hanel & Sturmauer, 2000, Desdevises *et al.*, 2002a) are found at these higher nodes. As discussed in Hanel & Sturmbauer (2000), this phylogenetic tree suggests that a phylogenetically confounding convergent morphological evolution has occurred in sparid fish.

Host size is related to *Lamellodiscus* species richness, as well as displacement. Fish with a migratory behaviour possess a higher richness in *Lamellodiscus* species. This suggests that new parasite species can be acquired in various geographical regions, and suggests a link between parasite species richness and host geographical distribution. This also suggests that parasites are not lost when hosts access new geographical locations. This is compatible with the same *Lamellodiscus* species being found throughout the Mediterranean Sea on various hosts (see Euzet *et al.*, 1993), and that external environmental

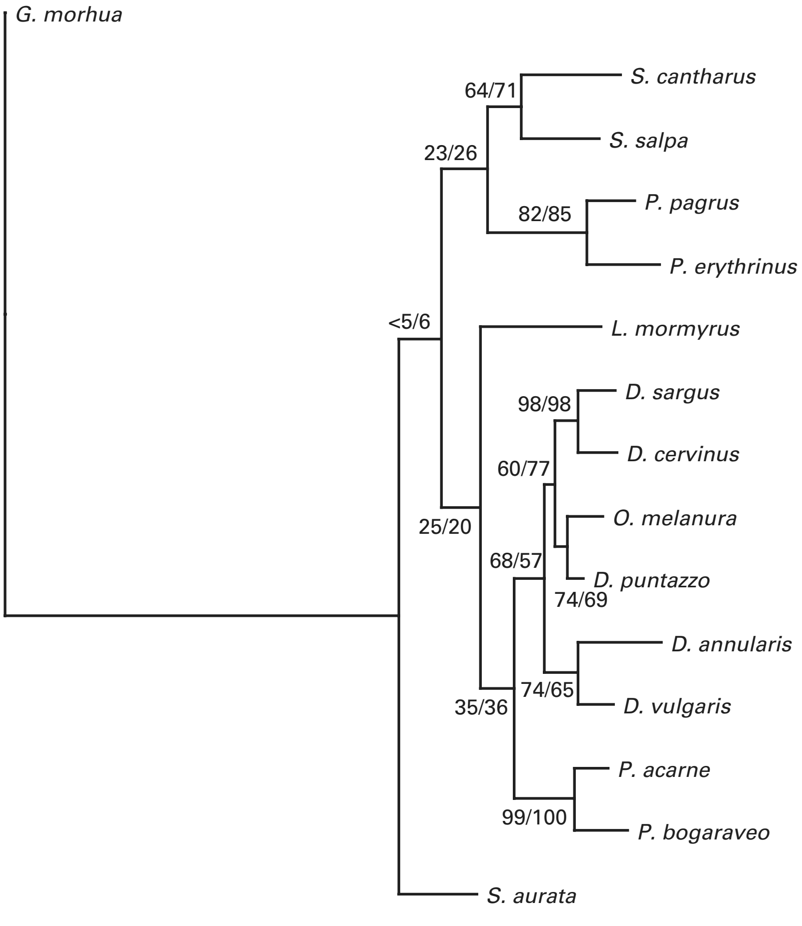

Fig. 1. Phylogenetic tree for 14 northern Mediterranean sparid fish species plus *Gadus morhua* (outgroup), reconstructed by maximum likelihood analysis of partial cytochrome-b and 16S mtDNA sequences. Numbers are bootstrap proportions (1000 replicates; neighbour-joining analysis/maximum parsimony analysis)

Table 3. Multiple regression on *Lamellodiscus* species richness on sparid fish species, relative to body size, abundance, displacement, social behaviour and phylogenetic inertia (represented by the first principal coordinate, PCo 1) as independent variables

	Variable	b	*P*	R^2	P (R^2)
Step 1	Body size	− 0.288	0.077		
	Abundance	− 0.145	0.187		
	Displacement	0.691	0.002		
	Social behaviour	0.264	0.086		
	PCo1	− 0.063	0.380	0.843	0.013
Step 2	Body size	− 0.324	0.043		
	Abundance	− 0.143	0.178		
	Displacement	0.709	0.002		
	Social behaviour	0.251	0.088	0.840	0.004
Step 3	Body size	− 0.352	0.030		
	Displacement	0.686	0.006		
	Social behaviour	0.182	0.135	0.824	0.003
Step 4	Body size	− 0.442	0.010		
	Displacement	0.693	0.006	0.800	0.001

Significant variables are selected via a backward elimination procedure: the least significant variable is removed at each step until all remaining variables are significant. b represents standardized partial regression coefficients. P indicates partial probability, and P(R^2) represents the global significance of the model.

factors may not be an obstacle to their presence on migratory fish hosts. This supports the hypothesis that host colonization by many monogeneans species is more a problem of opportunity than compatibility between host and parasite (Desdevises *et al.*, 2002a,b).

Host size is inversely related to parasite species richness: smaller fish species possess more *Lamellodiscus* species. Indeed, large sparid species, such as *Pagrus pagrus* or *Sparus aurata*, harbour very few *Lamellodiscus* species. This has been related to the solitary behaviour of these species and the lower probability of their sharing parasite species (Desdevises *et al.*, 2002a), but no statistical link with social behaviour was found here. Larger species are more rare and remain isolated from other sparid species, which is likely to decrease the chance of parasite exchange. The absence of a significant relationship with social behaviour may be due to the relatively low number of species considered. This inverse link between monogenean species richness and host size supports the idea that niches are generally far from being saturated in monogeneans (see Rohde, 1994; Morand *et al.*, 2002), and that this factor is not limiting for host colonization by these parasites. Interspecific competition has been suggested to be unimportant in most monogenean communities (Rohde, 1979, 1994; Simkova *et al.*, 2000). The present results support this hypothesis for the *Lamellodiscus*–Sparidae system, but not if all parasite species had been considered, as niche availability is generally limiting for endoparasites (Holmes, 1973; Morand *et al.*, 2000).

The absence of any statistical link between *Lamellodiscus* species richness and phylogeny (i.e. phylogenetic inertia) suggests that the formation of monogenean species assemblages is more under the influence of ecological than historical factors. In other words, hosts do not tend to harbour the same parasite species as those of their ancestors. Morand *et al.* (2002) emphasized the likely important influence of ecological relative to evolutionary factors in the structuring of monogenean communities and this is also in accordance with the hypothesis of Desdevises *et al.* (2002a) who hypothesized the existence of an opportunistic colonization behaviour in monogeneans.

The present results can be compared with those of Guégan *et al.* (1992) who also investigated determinants of monogenean species richness in fish and also found host size and host ecology to be important in parasite species richness in their system. However, Guégan *et al.* (1992) found that monogenean species richness is positively linked to host size and in particular to the increasing number of available niches corresponding to larger gill areas in larger fish. As the relationship between host size and monogenean species richness is the opposite in the present study, it can be hypothesized that the *Lamellodiscus*–Sparidae system is not saturated, unlike that described by Guégan *et al.* (1992) for species of *Dactylogyrus* in their cyprinid hosts. On the other hand, the host–parasite system is confined to freshwater, where the infection dynamics and parasite species richness are generally different from those in marine systems (see Marcogliese, 2001). It should also be noted that Guégan *et al.* (1992) did not take host phylogeny into account and this may lead to biased results (Harvey & Pagel, 1991). For example, Morand & Poulin (1998) found that a significant link computed from a cross-species analysis between parasite species richness and host body size disappears when host phylogeny is considered, and that the relationship between parasite species richness and host density is opposite in a non-phylogenetic compared to that in a phylogenetic approach.

Poulin (1997) found that hosts with a low parasite species richness tend to possess generalist parasites, i.e. parasitizing several host species, while hosts with high parasite species richness harbour more specialist parasites, i.e. using one host. In the present study, high species richness was associated with smaller hosts, and Desdevises *et al.* (2002b) found that in the same host–parasite system, specialist *Lamellodiscus* species tend to use large hosts. These results are the opposite to those of Poulin (1997): in the *Lamellodiscus*–Sparidae system in the Mediterranean Sea, species-rich communities are found on small hosts which are more parasitized by generalist parasite species. These inverse results may be due to the different scales at which these studies are carried out as the findings of Poulin (1997) are concerned with various parasite taxa over a large geographical scale, i.e. Canadian freshwater fish, thus emphasizing the need to consider the scale at which studies of this kind are performed.

References

Bakke, T.A., Harris, P.D., Jansen, P.A. & Hansen, L.P. (1992) Host specificity and dispersal strategy in gyrodactylid monogeneans, with particular reference to *Gyrodactylus salaris* (Platyhelminthes, Monogenea). *Diseases of Aquatic Organisms* **13**, 63–74.

Bell, G. & Burt, A. (1991) The comparative biology of parasite species diversity: internal helminths of freshwater fish. *Journal of Animal Ecology* **60**, 1047–1063.

Brooks, D.R. & McLennan, D.A. (1991) *Phylogeny, ecology, and behavior. A research program in comparative biology.* 441 pp. Chicago, Illinois, University of Chicago Press.

Caro, A., Combes, C. & Euzet, L. (1997) What makes a fish a suitable host for Monogenea in the Mediterranean? *Journal of Helminthology* **71**, 203–210.

Desdevises, Y. (2001) The phylogenetic position of *Furnestinia echeneis* (Monogenea Diplectanidae) based on molecular data: a case of morphological adaptation? *International Journal for Parasitology* **31**, 205–208.

Desdevises, Y., Jovelin, R., Jousson, O. & Morand, S. (2000) Comparison of ribosomal DNA sequences of *Lamellodiscus* spp. (Monogenea, Diplectanidae) parasitizing *Pagellus* (Sparidae, Teleostei) in the north Mediterranean Sea: species divergence and coevolutionary interactions. *International Journal for Parasitology* **30**, 741–746.

Desdevises, Y., Morand, S., Jousson, O. & Legendre, P. (2002a) Coevolution between *Lamellodiscus* (Monogenea) and Sparidae (Teleostei): the study of a complex host–parasite system. *Evolution* **56**, 2459–2471.

Desdevises, Y., Morand, S. & Legendre, P. (2002b) Evolution and determinants of specificity in the genus *Lamellodiscus* (Monogenea). *Biological Journal of the Linnean Society* **77**, 431–443.

Diniz-Filho, J.A.F., de Sant'Ana, C.E.R. & Bini, L.M. (1998) An eigenvector method for estimating phylogenetic inertia. *Evolution* **52**, 1247–1262.

Esch, G.W., Bush, A.O. & Aho, J.M. (1990) *Parasite communities: patterns and processes*. 304 pp. London, England, Chapman and Hall.

Euzet, L. (1984) Diplectanidae (Monogenea) parasites de poissons des Iles Kerkennah (Tunisie). *Archives de l'Institut Pasteur de Tunis* **61**, 463–474.

Euzet, L. & Oliver, G. (1966) Diplectanidae (Monogenea) des Téléostéens de la Méditerranée occidentale. III. Quelques *Lamellodiscus* Jonhston et Tiegs, 1922, parasites de poissons du genre *Diplodus* (Sparidae). *Annales de Parasitologie* **41**, 573–598.

Euzet, L. & Oliver, G. (1967) Diplectanidae (Monogenea) de Téléostéens de la Méditerranée occidentale. IV. Quelques *Lamellodiscus* Jonhston et Tiegs, 1922, parasites de poissons du genre *Pagellus* Cuvier, 1829 (Sparidae). *Annales de Parasitologie* **42**, 407–425.

Euzet, L., Combes, C. & Caro, A. (1993) *A check list of monogenea of Mediterranean fish*. Second International Symposium on Monogenea, Montpellier/Sète, France.

Farris, J.S., Kallersjo, M., Kluge, A.G. & Bult, C. (1994) Testing significance of incongruence. *Cladistics* **10**, 315–320.

Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.

Fiedler, K. (1991) Familie Sparidae. pp. 354–355 *in* Starck, D. (*Ed.*) *Lehbruch der Speziekken Zolologie. Tejl 2: Fishe.* Jena, Gustav Fisher Verlag.

Gregory, R.D. (1990) Parasites and host geographic range as illustrated by waterfowl. *Functional Ecology* **4**, 645–654.

Gregory, R.D., Keymer, A.E. & Harvey, P.H. (1991) Life history, ecology and parasite community structure in Soviet birds. *Biological Journal of the Linnean Society* **43**, 249–262.

Guégan, J.F., Lambert, A., Lévêque, C., Combes, C. & Euzet, L. (1992) Can host body size explain the parasite species richness in tropical freshwater fishes? *Oecologia* **90**, 197–204.

Hanel, R. & Sturmbauer, C. (2000) Multiple recurrent evolution of trophic types in northeastern Atlantic and Mediterranean seabreams (Sparidae Percoidei). *Journal of Molecular Evolution* **50**, 276–283.

Harvey, P.H. & Pagel, M.D. (1991) *The comparative method in evolutionary biology.* 248 pp. Oxford, Oxford University Press.

Holmes, J.C. (1973) Site selection by parasitic helminths: interspecific interactions, site segregation and the importance to development of helminth communities. *Canadian Journal of Zoology* **51**, 333–347.

Jousson, O., Bartoli, P. & Pawlowski, J. (2000) Cryptic speciation among intestinal parasites (Trematoda: Digenea) infecting sympatric host fishes (Sparidae). *Journal of Evolutionary Biology* **13**, 778–785.

Lapointe, F.-J. (1998) How to validate phylogenetic trees? A stepwise procedure. pp. 71–88 *in* Hayashi, C., Ohsumi, N., Yajima, K., Tanaka, Y., Bock, H.H. & Baba, Y. (*Eds*) *Studies in classification, data analysis, and knowledge organization: data science, classification, and related methods*. Tokyo, Springer.

Legendre, P. & Legendre, L. (1998) *Numerical ecology.* 2nd English edn. Development in Environmental Modelling, 20. 870 pp. Amsterdam, Elsevier.

Marcogliese, D.J. (2001) Pursuing parasites up the food chain: implications of food web structure and function on parasite communities in aquatic system. *Acta Parasitologica* **46**, 82–93.

Martins, E.P., Diniz-Filho, J.A. & Housworth, E.A. (2002) Adaptation and the comparative method: a computer simulation study. *Evolution* **56**, 1–13.

Morand, S. & Harvey, P.H. (2000) Mammalian metabolism, longevity and parasites species richness. *Proceedings of the Royal Society of London B* **267**, 1999–2003.

Morand, S. & Poulin, R. (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* **12**, 717–727.

Morand, S., Cribb, T.H., Kulbicki, M., Rigby, M.C., Chauvet, C., Dufour, V., Faliex, E., Galzin, R., Lo, C.M., Lo-Yat, A., Pichelin, S. & Sasal, P. (2000) Endoparasite species richness of New Caledonian butterfly fishes: host density and diet matter. *Parasitology* **121**, 65–73.

Morand, S., Simkova, A., Matejusova, I., Plaisance, L., Verneau, O. & Desdevises, Y. (2002) Investigating patterns may reveal processes: evolutionary ecology of ectoparasitic monogeneans. *International Journal for Parasitology* **32**, 111–119.

Oliver, G. (1969a) Recherches sur les Diplectanidae (Monogenea) parasites de Téléostéens du Golfe du Lion. II. Lamellodiscinae nov. sub. fam. *Vie et Milieu* **20**, 43–72.

Oliver, G. (1969b) Recherches sur les Diplectanidae (Monogenea) parasites de Téléostéens du Golfe du Lion. III. Biologie. *Vie et Milieu* **20**, 397–419.

Oliver, G. (1973) *Lamellodiscus obeliae* n. sp. une nouvelle espèce de Diplectanidae (Monogenea, Monopisthocotylea) parasite de *Pagellus centrodontus* (Delaroche, 1809) (Pisces, Sparidae). *Zeitschrift für Parasitenkunde* **41**, 103–108.

Oliver, G. (1974) Nouveaux aspects du parasitisme des Diplectanidae Bychowsky, 1957 (Monogenea, Monopisthocotylea) chez les Téléostéens Perciformes des côtes de France. *Comptes Rendus de l'Académie des Sciences de Paris* **279**, 803–805.

Orrell, T.M. & Carpenter, K.E. (2004) A phylogeny of the fish family Sparidae (porgies) inferred from mitochondrial sequence data. *Molecular Phylogenetics and Evolution* **32**, 425–434.

Page, R.D.M. & Charleston, M.A. (1998) Trees within trees – phylogeny and historical associations. *Trends in Ecology and Evolution* **13**, 356–359.

Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818.

Poulin, R. (1991a) Group-living and infestation by ectoparasites in passerines. *Condor* **93**, 418–423.

Poulin, R. (1991b) Group-living and the richness of the parasite fauna in Canadian freshwater fishes. *Oecologia* **86**, 390–394.

Poulin, R. (1995) Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* **65**, 283–302.

Poulin, R. (1997) Parasite faunas of freshwater fish: the relationship between richness and the specificity of parasites. *International Journal for Parasitology* **27**, 1091–1098.

Poulin, R. & Morand, S. (1999) Geographical distances and the similarity among parasite communities of conspecific host populations. *Parasitology* **119**, 369–374.

Ranta, E. (1992) Gregariousness versus solitude: another look at parasite faunal richness in Canadian freshwater fishes. *Oecologia* **89**, 150–152.

Rohde, K. (1979) A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites *American Naturalist* **114**, 648–671.

Rohde, K. (1994) Niche restriction in parasites: proximate and ultimate causes. *Parasitology* **109**, S69–S84.

Saitou, N. & Nei, M. (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* **4**, 406–425.

Schmidt, G.D. & Roberts, L.S. (1989) *Foundations of parasitology*. 4th edn. 750 pp. St Louis/Toronto/Boston/-Los Altos, Times Mirror/Mosby College Publishing.

Simkova, A., Desdevises, Y., Gelnar, M. & Morand, S. (2000) Coexistence of nine gill ectoparasites (*Dactylogyrus*: Monogenea) parasitising the roach (*Rutilus rutilus* L.): history and present ecology. *International Journal for Parasitology* **30**, 1077–1088.

Swofford, D.L. (2002) *PAUP*: Phylogenetic analysis using parsimony and other methods*. Version 4.0d10. Champaign, Illinois, Illinois Natural History Survey.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The ClustalX Windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **24**, 4876–4882.

Whitehead, P.J.P., Bauchot, M.L., Hureau, J.C., Nielsen, J. & Tortonese, E. (1986) *Fishes of the North-eastern Atlantic and the Mediterranean*. Vol. III. pp. 1008–1473. Paris, UNESCO.

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