INTRODUCTION

Coyne (2007) has recently reviewed the reasons why sympatric speciation is so controversial and why this mode of speciation is so contested in evolutionary biology. Sympatric speciation involves the splitting of an ancestral species into two or more reproductively isolated groups, the incipient species, without the need of geographical isolation as involved in allopatric speciation. Importantly, the speciation should occur when these incipient species are still in contact and are able to exchange genes. Interestingly, in his review, Coyne (2007) cited three studies on host-parasite systems (Berlocher & Feder 2002, Sorenson et al. 2003, Simková et al. 2004) among five examples of sympatric speciation (Schliewen et al. 1994, Savolainen et al. 2006), suggesting by this that host-parasite systems offer convincing models of sympatric speciation, according to Coyne (2007). However, inferring mode of speciation does not help to depict the mechanism of sympatric speciation and theoretical model of speciation can be useful to investigate the conditions of sympatric speciation in parasites, as it has been already done for free-living organisms. Finally we aim at highlighting that diversification of parasites through intra-host speciation is maybe a prevalent mode of speciation in parasites, as the numerous number of parasite species flocks suggest, and that parasites are also good models for investigating the mechanisms of sympatric speciation.

The great majority of studies on host-parasite associations, either theoretical or empirical, have then focused on cospeciation and host-switch minimizing the importance of sympatric speciation, a mode of speciation that the four conditions required to recognize a case of sympatric speciation, according to Coyne (2007). However, the relative importance in number of congeneric parasite species or parasite flocks has been described earlier in the parasitological literature (Schad 1963, Gusev 1995, Beveridge et al. 2003, Boumer & Morand 2003, Matthee et al. 2004).

MODES OF SPECIATION IN PARASITES

Earlier, it has been proposed that parasite phylogeny mirrors host phylogeny, i.e. Farenholz’ rule, as summarized by Klassen (1992) in a review on the history of host-parasite coevolution studies. Indeed, speciation of parasites is often viewed to occur via co-speciation (Page 2003, Clayton et al. 2004). Using a phylogenetic framework, cospeciation in host-parasite systems was first demonstrated for pocket gophers and their chewing lice (Hafner & Nadler 1988, Hafner et al. 1994, Reed & Hafner 1997) followed by several studies on various host-parasite associations, such as primates and their pinworms (Hugot 1999).

Several methodological development and improvement of statistical tests of cospeciation have been pro-
posed: Brooks Parsimony Analysis (Brooks & McLennan 1991), tree reconciliation (Charleston 1998, Page & Charleston 1998, Page 2003, Ronquist 1995), global fit methods (Johnson et al. 2003; Legendre et al. 2002) (see Paterson & Bank 2001, Desdevises 2007, de Vienne et al. 2007). Allopatric parasite speciation was suggested to follow the geographical isolation of their hosts as a plausible mechanism of cospeciation (Weckstein 2004). However, the mechanisms of parasite adaptation following the cospeciation events were rarely investigated. Cospeciation events were described in several host-parasite systems: chewing lice and pocket gophers (Hafner et al. 1994), pinworms and primates (Hugot 1999), Pneumocystis spp. and primates (Hugot et al. 2003), whereas other studies failed to find extensive cospeciation, such as between chewing lice and penguins (Banks et al. 2006).

In several host-parasite systems, there were no indices of widespread cospeciation. This leads to a key question for evolutionary biologists: why and when do parasites fail to speciate in response to host speciation (Johnson et al. 2003).

Host-switch events have been exemplified in several host-parasite systems (Desdevises et al. 2002), although host shifts can produce congruent host and parasite phylogenies (Percy et al. 2004, Huyse & Volckaert 2005, de Vienne et al. 2007). Speciation following host switch is also widely observed in fish monogeneans (Desdevises et al. 2002, Zietara & Lumme 2002, Huyse & Volckaert 2005).

Finally, “missing the boat” or “extinction” was proposed to explain the lack of incipient parasite species in incipient host species. This explanation refers to the hypothesis that the ancestral parasite species has missed one incipient host species during the host speciation process (Paterson & Gray 1997, Page 2003).

CONGENERIC SPECIES IN PARASITES

Multiple parasite congeners have been earlier exemplified as evidence for radiation of species-flocks (Schad 1963, Petter 1966, Inglis 1971, Matthee et al. 2005). Kennedy & Bush (1992) and Poulin (1999) have surveyed published studies and found that congeneric helminths were quite common in parasite communities. For example, several congeneric species are well-known: oxyurid nematodes of tortoises (Schad 1963, Bouamer & Morand 2003), strongyloid nematodes of horses and elephants (Bucknell et al. 1996), cloacinids of kangaroos (Beveridge & Spratt 1996) and monogeneans of fish (Pariselle et al. 2003, Šimková et al. 2006).

Poulin (1999) tested the influences of ecological determinants, such as body size, host density or latitude, as explanatory factors of species richness in congeneric parasite flocks parasitizing birds and mammals. Although Poulin (1999) found that aquatic bird species tend to harbour more congeneric parasites than terrestrial birds, the main result was found in mammals. Poulin (1999) found that large-bodied mammal species, or those living at low latitudes, harbour more congeneric parasites than small-bodied mammals, or than those from higher latitudes. This finding suggests that the size of the host, i.e. the host gut in this study, is a good predictor for the diversification of congeneric species. Large-bodied hosts seem to offer more opportunities for intra-host speciation than small-bodied hosts. Using congeneric parasites of fish, Šimková et al. (2001) also showed that large-bodied fish harbour more congeneric monogenean species than small-bodied fish. These observations confirm that the size of the “host as an island” is an important feature allowing the coexistence of several parasite species. A possible explanation is that larger-bodied hosts have larger organs (guts in mammals, gills in fish) that offer more space but also more micro-environments that allow parasites to exploit specifically.

Nevertheless, as emphasized by Poulin (1999) these communities of congeneric species may represent real species flocks, being the product of the radiation of an ancestral taxon. Strict habitat selection is supposed to lead to a higher frequency of sympatric speciation in parasite species than in free-living animals according to de Meuïs et al. (1995). Multiple congeners can also be the result of several independent host-switch events by congeneric parasites that have evolved in other hosts (Paterson & Gray 1997), Vickery & Poulin (1998) as well suggested that intra-host speciation could explain the occurrence of congeneric parasite species in the same host species. Phylogenetic information is then needed to discriminate among these hypotheses.

WHAT IS SO DIFFICULT IN SYMPATRIC SPECIATION? AND HOW TO TEST ITS EXISTENCE?

Coyne (2007) emphasized that sympatric speciation is “hard to achieve because of the genetic recombination that occurs when incipient species interbreed. This recombination breaks up the correlation between co-adapted groups of genes that is necessary for species to form”. There is a cost of hybridization due to the production of offspring with intermediate phenotype of intermediate fitness (Kondrashov & Shpak 1998, Kondrashov & Kondrashov 1999). We should also take into consideration that most theoretical models seem to show that sympatric speciation occur under very restrictive conditions in real biological situations (Coyne & Price 2000, Gourbière 2004, Jiggins 2006).

Establishing sympatric speciation requires four conditions according to Coyne (2007):

- (i) the species must be sympatric; the incipient species could have speciated sympatrically and subsequently
have become allopatric; reproductive isolation, preferably based on genetic differences;

- (ii) the sympatric species must show substantial

Fig. 1. - Tanglegram of Dactylogyrus and cyprinid species (from Šimková et al. 2004). Intrahost duplications are depicted on the trees. Dactylogyrus speciation by intrahost duplication supported by bootstrap percentage greater than 50 are given in bold. Potential coevolution events are indicated by a, b, and c.
(iii) the sympatric taxa must be sister species; however, this criterion could be difficult to meet as any hybridization between taxa will render them closely related;

(iv) the biogeographic and evolutionary history of the groups must make the existence of an allopatric phase very unlikely; a hard task as it requires to demonstrate that the incipient species were never geographically isolated.

Coyne (2007) suggested that cases of sympatric speciation can be found on islands, such as oceanic islands or lakes, by searching for closely related species. Endemic sister species of mobile organisms contained in these islands are likely to have evolved without physical isolation (i.e. cichlid fish of African lakes). He suggested that other cases can be found in a single host species that harbours sister species of host-specific parasites. This corresponds to sympatric speciation within a host, with the host considered as an island for its parasites (Kuris et al. 1980).

AN EXAMPLE OF SYMPATRIC (INTRA-HOST) SPECIATION: DACTYLOGYRUS SPP. OF CYPRINID FISH

Dactylogyrus species are a group of monogenean gill parasites that are highly specific to freshwater fish of the family Cyprinidae. Šimková et al. (2004) sampled Dactylogyrus species from cyprinids in Europe, and using molecular data proposed a phylogeny of most Dactylogyrus species from Central Europe. They used TreeMap 1.0 (Page 1994) to depict the host-parasite associations using a Dactylogyrus phylogenetic tree inferred from the analysis of molecular data and a cyprinid tree (Fig. 1). The comparison of host and parasite phylogenetic relationships indicated that a high number of intra-host speciation occurred in Dactylogyrus lineages. Then, parasite diversification can be mainly explained by these speciation events that are correlated to strict host specificity.

The four conditions of Coyne (2007) seem to be met:

(i) the parasite species are sympatric, they live on the gills of the same host species, although they are not distributed randomly on the gills (see below);

(ii) reproductive isolation is associated with genetic isolation;

(iii) the congeneric parasites are sister species as revealed by the tanglegram (Fig. 1);

(iv) the biogeographic and evolutionary history of the cyprinid hosts make the existence of an allopatric phase for these congeneric parasite species very unlikely and limited to three co-speciation events depicted by TreeMap. However, it remains possible that some Dactylogyrus species have speciated allopatrically in geographically isolated fish populations, and then re-infected fish hosts after secondary contact between host populations. This scenario implies that monogeneans evolve more rapidly than their hosts. Allopatric speciation may imply changes in host-specificity of monogeneans that should first increase their host range by infecting fish populations in secondary contacts and second decrease their host range to reach the strict host-specificity currently observed. As strict host-specificity has been shown to be ancestral in most Dactylogyrus lineages (Šimková et al. 2006), this renders the latter scenario unlikely.

As mentioned above, monogeneans are not randomly distributed on fish gills. They show preferred positions on gills, which were investigated by Šimková et al. (2000, 2006). For each parasite individual, position on gill arch, gill segment and gill area was recorded. The preferred position, or niche, corresponds to the sector where the maximum number of parasite individuals was found. The preferred niche (gill arch, segment and area) was mapped onto the phylogenetic tree using MacClade with Farris optimization (Maddison & Maddison 1992) (Fig. 2). Dactylogyrus species from one lineage, parasitizing the same host, then recognized as a case of intra-host speciation, were separated by their position (arch, segment or area) on fish gills. If we consider changes, we note that no sister species have identical niches for all three gill dimensions. At least one of the niche parameters (arch, segment or area) has changed between these species. Finally, Šimková et al. (2004, 2006) hypothesized that this mode of sympatric speciation should be closely related to morphological evolution of attachment organs.

COMPETITIVE SPECIATION AS THE MECHANISM OF INTRA-HOST SPECIATION?

Competitive speciation is based on theoretical models in which a quantitative ecological trait is under disruptive selection generated by frequency and density dependent intra-specific competition (Dieckmann et al. 2004, Coyne & Orr 2004). This ecological trait can pleiotropically affect mate choice in some models (e.g. Gourbière 2004), while other models describe the evolution of mating preferences according to the ecological trait under natural selection (Bürger et al. 2006). All these theoretical models refer to the ecological notion of character displacement (Taper & Case 1985). Gourbière et al. (unpublished) using Dactylogyrus species have investigated the conditions for within-host competitive speciation of parasites and shown that they are exactly the same as the conditions for competitive diversification of non-parasitic species (Dieckmann & Doebeli 1999, Doebeli & Dieckmann 2000). These conditions are surprisingly robust whatever the life-histories of the considered organisms, parasites or free-living, and moreover are quite easy to get.

How and when competitive speciation can play a role in parasite diversification may depend on the host, and more precisely on the potential niches that the host can offer for parasites to live on. Competitive speciation may
Fig. 2. - Mapping of preferred position of Dactylogyrus on fish gills (upper drawing) onto the Dactylogyrus phylogeny (from Šimková et al. 2004), lower drawings from left to right: arc, segment, area of fish gill.
also depend on the parasite itself, and on the quantitative traits that are susceptible to be affected.

One additional difficulty with intra-host speciation is that the opportunity to observe it on the tanglegram depends on additional host features. For instance, the ecology of the hosts, such as diet preferences or spatial distribution, can change the actual number of host-switch events, which will change the possibility to detect intra-host speciation. This is simply because a high rate of host-switches would tend to shorten the time period where the monophyletic signal can be detected after within-host adaptive radiation (see also the link between host ecology and parasite specificity, Šimková et al. 2006). This may explain why intra-host speciation should be more easily observed in freshwater fish, where fish species are more isolated “as islands” from each others due to the river systems or ecological specialisation. This isolation may prevent host-switching events.

Parasites should show ecological traits linked to potential competition and to reproductive isolation. Coexisting monogenean species have more similar morphology in attachment organs when they live in close contact on gills, but are more dissimilar in the size of their copulatory organs (Rohde & Hobbs 1986, Rohde 1989, Šimková et al. 2002). Morphological evolution of the attachment organ can be viewed as the result of adaptive processes for selection of the position on gill of a given host fish, whereas morphological evolution of the reproductive apparatus can be viewed as the result of the evolution of pre-zygotic barriers among incipient species (Morand et al. 2002, Jarkovský et al. 2004). Competition process may have lead to switch in the “niche position space” on the gills, whereas pre-zygotic barriers have helped to maintain the incipient species integrity.

CONCLUSION AND SUGGESTIONS FOR FURTHER RESEARCH

The two paradigms of parasite speciation, cospeciation and host-switch, have focused the attention of evolutionary biologists on specific cases of host-parasite models, where the number of congeneric species living on one host species are often low. Investigating the process of intra-host speciation in parasites implies to focus on the study of parasite flocks that are far from being rare (Kennedy & Bush 1992, Poulin 1999).

Here we suggest that sympatric speciation, or intra-host speciation, represents a considerable process of speciation in gill monogeneans. This mode of speciation is potentially more frequent as it is obscured by host-switch favoured in rich-host communities, i.e. marine environment for example (Desjeuxes et al. 2002, Plaisance et al. 2005), or where no ecological barriers may limit host-switch events such as hydrological basins in freshwater environment (Pariselle et al. 2003). Intra-host speciation may be more common in other parasitic systems as new studies are conducted (Giraud 2006, Lopez-Villavicencio et al. 2007, Pérez-Tris et al. 2007).

Future studies should investigate the mechanisms that promote sympatric speciation. For this we need theoretical models, biological investigations and comparative tests. Competitive speciation models offer the way to theoretically study intra-host speciation. Species diversification is mechanically associated with post-zygotic isolation, as hybrids with intermediate phenotype should experience strong competition from individuals of both incipient species (i.e. the cost of hybridization). This, in turns generates the conditions for the evolution of pre-zygotic isolation. The conditions for the evolution of pre-zygotic isolation may be more restrictive than the conditions for evolutionary diversification. This has actually been loosely reported in previous studies investigating reinforcement by evolution of assortative mating with respect to either the ecological trait under disruptive selection or a neutral marker trait (Gourbière & Mallet 2005). We need to adapt these theoretical models to the parasitic mode of life. Second, we need to find the traits that promote the coexistence of congeneric species on the same hosts. Candidate traits are haptor morphology for gill monogeneans (Šimková et al. 2001). However, we should be aware that we are far from knowing the traits promoting the coexistence of other parasites such as gut nematodes. Next, we should show whether these traits are only related to coexistence or to host micro-environment exploitation. Are these traits involved in the speciation process? The traits associated with pre-zygotic isolation and assortative mating seem to be good candidates for investigating the mechanism of intra-host speciation processes. Last, we need to perform comparative analyses using a good phylogenetic framework (Morand & Poulin 2003), which may allow us to test the relevant hypotheses.

Finally, paraphrasing Jiggins (2006) and knowing the difficulty of investigating the case of speciation, we should abandon the assumption that allopatric speciation is the “null hypothesis” as we always refer to the hypothesis of speciation with gene flow. Future research should concentrate on the more proximal causes of speciation and on the potential traits causing divergence.

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