

Santa Rosalia Revisited: or Why Are There So Many Kinds of Parasites in 'The Garden of Earthly Delights'?

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As is the case for free-living species, a very large number of parasitic species are not described adequately by the biological species concept. Furthermore, Thierry de Meeûs, Yannis Michalakis and François Renaud argue that because hosts represent a highly heterogeneous and changing environment as well as a breeding site, favouring the association of host-adaptation and host-choice genes, sympatric speciation may occur frequently in parasitic organisms. Therefore, parasites appear to be ideal biological models for the study of ecological specialization and speciation. Beyond the relevance of such considerations in fundamental science, the study of the origin and evolution of parasite diversity has important implications for more applied fields such as epidemiology and diagnosis.

The biological species concept (BSC) which emphasizes the role of reproductive isolation¹ remains widely used despite the fact that it cannot account satisfactorily for a large number of biological examples². Furthermore, because it focuses on the outcome and not the process, it has been detrimental to studies on mechanisms of speciation³ and, in particular, it has served as a background to the main arguments against the existence of sympatric speciation. Santa Rosalia was first mentioned by Hutchinson⁴ to provide a functional explanation for the origin and apportionment of animal species. Several authors subsequently referred to him in order to discuss the existence of non-allopatric modes of speciation^{5,6}.

As mentioned previously by Lymbery^{7,8}, for some parasites the BSC has many limitations. Indeed, it focuses on reproductive isolation as the unique criterion to delimit the species boundaries. Thus, the BSC confuses one consequence and its cause: reproductive isolation and the processes leading to it³. Given these limitations, several alternatives to the BSC have been proposed^{2,3,8}.

Many examples illustrate the inadequacy of the BSC. Indeed, large parts of the living world lie outside the BSC's logical domain, because they display either 'too little' or 'too much' sex³. Obviously, the BSC is applicable only to sexually reproducing organisms⁹. Moreover, self-mating and sib-mating organisms and any other closed system of mating cannot be accounted for satisfactorily by the BSC. In addition, many species are able to hybridize with others without losing their ecological and genetic identities through time^{3,10}. Paradoxically, in some cases it is the hybridization itself that leads to new species. Indeed, many polyploid lineages are known to result from a hybridization event between two different species¹¹.

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Limitations of the BSC for parasites

Parasitic organisms constitute a large proportion of the cases problematical to the BSC. Many parasite taxa exhibit extremely restricted cross fertilization. Such restrictions may be due to extreme rates of clonal reproduction, selfing or biparental inbreeding such as sib-mating. Parthenogenesis is very well documented in numerous families of nematodes parasitic on plants and animals¹². The large controversy concerning the clonality of many microparasites illustrates clearly the opposition between parasites and the BSC¹³⁻¹⁵. The most spectacular examples of selfing lie within the cestode group. *Taenia solium*, which is nearly always found alone in the human intestine, can only self-reproduce¹⁶. In the *Cyclorchida* genus, because of anatomical constraints of the genitalia, self-fertilization is the only possibility¹⁶. Sib-mating is also often encountered among parasites. For instance, in many hymenopteran parasitoid wasps, such as *Nasonia vitripennis*, mating occurs only between brothers and sisters¹⁷. Finally, many species undergo phases of asexual reproduction and sib-mating. For example, in many helminths the intermediate host is infected only by one individual, which undergoes asexual multiplication. The products of this asexual multiplication in the intermediate host are likely to mate together in the definitive host. Such a mating system, genetically synonymous with selfing, occurs in cestodes⁸ and trematodes¹⁸. Applying the BSC to any of the previous examples would lead us to consider each individual as a single species and each egg hatching as a speciation event.

'Too much' sex, however, is also encountered in parasites. The most well-known example concerns the genus *Schistosoma*, where hybridizations have been described between different species^{19,20}. This is also known to occur between *Echinostoma* species²¹. Furthermore, bacteria can exchange DNA even between distant 'species'^{22,23}. Hybridization itself may also lead to speciation through polyploidization in parasites as, for example, in *Paragonimus* flukes²⁴, thus fully contradicting the BSC. This process is probably largely overlooked in parasites and the few examples available concern human parasites.

Sympatric speciation in parasites

All these examples illustrate the fact that the BSC cannot be applied to a large number of parasite species. These considerations are, arguably, only semantic, requiring a solution only for the exceptions. However, BSC, by definition, brings problems of another order: it may lead to the mechanisms

* 'The Garden of Earthly Delights' refers to the triptych by Hieronymus Bosch (c. 1500; Museo del Prado, Madrid) and, particularly, to its right panel which exhibits an impressive collection of tormenting creatures that a biologist could recognize as the likely outcomes of recombination, hybridization and mutation combined with diversification.

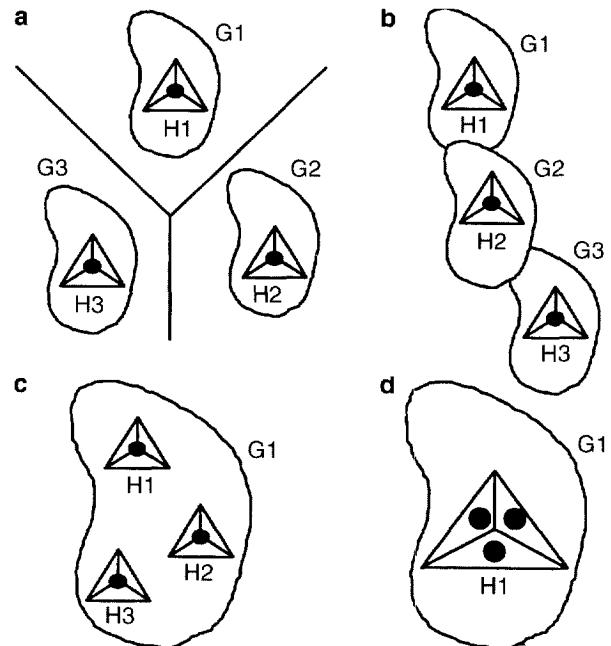
responsible for reproductive isolation being overlooked³. Indeed, even if many sexually reproducing species can be recognized through the BSC, one can consider that the reproductive isolation they display against other species originated from other processes, independent of those that led to such an isolation. Thus, any evidence of reproductive isolation between two closely related species provides no information on the processes responsible for such an outcome. The real problem here is less to testify the existence of reproductive isolation than to understand the underlying mechanisms. When speciation is allopatric, reproductive isolation is coincidental: while the different gene pools are allopatric, selection will not act in favour of isolating mechanisms. Characters diverge between gene pools either by chance, or to adapt to different environments or genomic composition. Reproductive isolation on secondary contact may arise only coincidentally to this divergence. Selection for such isolating mechanisms comes into action only after secondary contact, ie. when different genetic entities are sympatric.

Under the BSC, the factors responsible for reproductive isolation in general play no direct role in species divergence³; therefore, all theoretical attempts using the BSC as a basis have failed to describe sympatric speciation as a probable event^{5,25}. Indeed, the evolution of reproductive isolation *per se* is unlikely because it will behave as a deleterious character when rare, ie. in any case at the initial stage of the process. Alternatively, sympatric speciation may occur without the need to invoke reproductive isolation, through adaptive polymorphism and habitat preference²⁶. As a recent study shows²⁷, the result of these mechanisms may be reinforced by any non-habitat-associated assortative mating. This process has been supported by some experimental work²⁸ but the most convincing evidence is provided by the natural example of the phytophagous insect *Rhagoletis pomonella*²⁹ – a parasite.

Because parasites provide particular situations, Box 1 illustrates the difference between true allopatric and true sympatric situations found in host-parasite systems. Allopatric speciation alone can hardly account for the diversity of unambiguous species of related parasites often encountered in a single host (Fig. 1). Considering the parasitological literature this situation is far from marginal. Among the platyhelminths, the monogeneans and cestoda provide the most striking examples. In the Tchad Basin (West Africa) the characid fish *Alestes nurse* is known to harbour on its gills eight monogenean species of the *Anulotrema* genus, each of which displays specific genitalia (Fig. 1). These parasites, as well as their host, live only in this area so that their divergence and speciation probably occurred in sympatry. In the Mediterranean, the gills of the fish *Liza saliens* (Mugilidae) are parasitized by four species of *Ligophorus*. In both cases, different parasite species are distributed non-randomly on different parts of the gills (Fig. 1). Niche differentiation and specialization most likely led to speciation of these parasites on the same host species in a single geographical area. Among the Cestoda, four species of *Acanthobothrium* are described in the spiral valve of the stingray *Dasyatis longus* from the Gulf of Nicoya (Costa Rica)³⁰.

Other examples can be found among terrestrial arthropods (lice). The bird *Ibis falcinellus* is parasitized

Box 1. Concepts of Allopatry and Sympatry in Parasitic Organisms



Different entities will be allopatric only if isolated geographically. Individuals belonging to allopatric groups cannot interact. This is the case when different parasite species live on different host species in areas where hosts are separated by physical barriers (a; solid lines), or in areas where vicariant host species replace one another without any obvious physical barriers (b). On the contrary, when encountered in the same geographical areas, such entities will be considered sympatric, even if exploiting different resources. Indeed, in such co-existing groups, individuals may still interact during their life cycle. For example, all helminths parasitizing the vertebrates living in a pond are sympatric, because of all the existing ecological interconnections between the hosts and their parasites (c). More spectacular sympatric cases arise when parasites specialize on different organs of the same host species (d). G, geographical areas; H, host species (triangles), partitioned into different organs (internal triangles); closed circles represent parasites.

by at least seven species of mallophagous insects, each of which is specialized on a single feather type³¹. Less spectacular in diversity, but necessarily recent, is the case of the three species of human lice³².

Furthermore, the most relevant evidence of ongoing sympatric divergences comes from the parasitological literature. In the Caribbean, the acquisition of a murine host by the human parasite *Schistosoma mansoni* leads to an adaptive divergence depending on the periodic behaviour of the host towards water³³. The sea louse *Lepeophtheirus europaeensis* also displays a sympatric divergence between the two flatfishes it parasitizes in the Mediterranean (brill and flounder) – a supposedly recent phenomenon³⁴. However, the better-documented studies come from insect parasites of plants^{35–38}. Among these, *Rhagoletis pomonella* represents a well-studied model^{29,39}.

When one considers the realm of microparasites, reproductive isolation appears irrelevant as a mechanism for discriminating species. The tremendous diversity observed in groups such as the yeast *Candida*

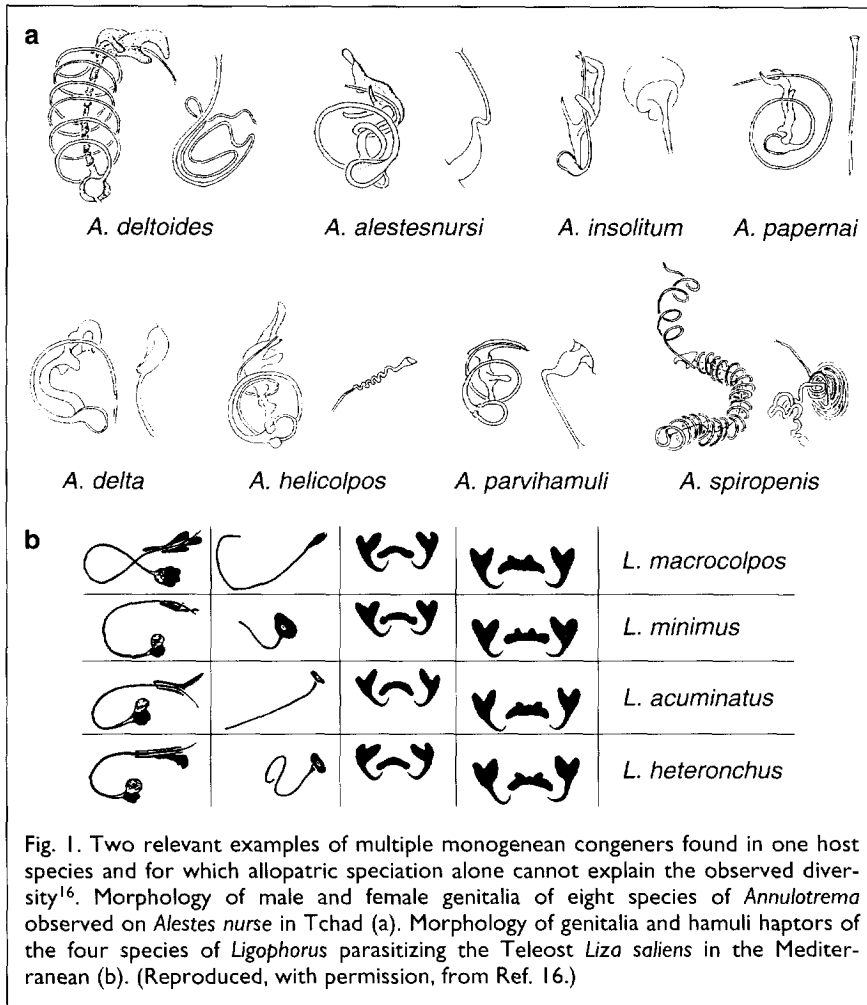


Fig. 1. Two relevant examples of multiple monogenean congeners found in one host species and for which allopatric speciation alone cannot explain the observed diversity¹⁶. Morphology of male and female genitalia of eight species of *Annulotrema* observed on *Alestes nurse* in Tchad (a). Morphology of genitalia and hamuli haptors of the four species of *Ligophorus* parasitizing the Teleost *Liza saliens* in the Mediterranean (b). (Reproduced, with permission, from Ref. 16.)

*albicans*¹⁶ suggests other modes of speciation instead of the classical allopatric model.

Does the parasitic way of life favour phylogenetic diversification?

Parasitism represents the conquest of life by life. The living environment evolves continuously. Thus, in order to persist in their living environments parasites must continuously adapt to their hosts. Hosts represent a major part of the ecological needs of their parasites (habitat, resource, etc.)⁴⁰. Hosts may represent many different kinds of resources and habitats (communities, species, populations, cohorts, sexes, individuals, organs, cells and molecules). Furthermore, hosts develop defences against such intruders, by behavioural, physiological and demographic means. Such defences impose an additional source of selective and diversifying pressures on parasites. Such continuous mutual aggressions resulting from the never-ending modifications of the living environment have largely shaped the life history traits and the evolutionary pathways in host-parasite systems (Red Queen concept)⁴¹.

The potential number of diversifying factors is much larger for parasitic organisms than for free-living organisms. All living species are involved in parasitism, either as parasites or as hosts⁴² and, as suggested by Timm and Clauson⁴³, parasites constitute the main part of the known species diversity. That the parasitic way of life might be a diversifying

factor is supported by comparative analyses of herbivorous insects. Phytophagy is encountered in only nine of the 13 orders of insects⁴⁴, but these orders account for approximately half of all insect species. Furthermore, phytophagous taxonomic groups are significantly more speciose than homologous groups of the same evolutionary age with a non-parasitic feeding habit⁴⁴. A possible explanation for this diversifying role of parasitism may lie in the fact that sympatric speciation is much more likely in parasitic species. Indeed, as stated previously, hosts provide ample opportunities for niche diversification among parasite populations, a necessary condition for sympatric speciation. Thus, sympatric speciation may play a much more central role in parasite evolution and evolutionary biology as a whole, with parasites representing ideal biological models for the study of ecological specialization and speciation mechanisms.

In the face of this acute potential for diversification, hosts have failed to eliminate all their parasites. For instance, even though mankind has managed to eliminate (almost) all of its competitors and predators, current knowledge indicates that it has been unable to

eliminate any of its parasites (smallpox being the exception that proves the rule). This is illustrated by modern prophylactic campaigns against malaria that are followed by the emergence of more and more *Plasmodium* strains resistant to nivaquine. As previously underlined⁴⁵, this genetic variability is crucial in both therapy and susceptibility to immune attack. There is a need to obtain the most precise knowledge of parasite diversity before developing therapeutics or vaccines. In the same way, the identification of the existing diversity of parasitic organisms must be taken into account in epidemiological surveys. This may allow us to discriminate more effectively, within parasite communities, those that are pathogenic and those that are not. This can be illustrated by the genetic divergences found between strains of *C. albicans*, which are comparable to that existing between the different mammalian species of the same genus¹⁶. Moreover, genetic distances between *C. albicans* sampled in one human host⁴⁶ exceeded that seen between great apes and humans⁴⁷, which diverged 5–7 million years ago⁴⁸. In addition, when compared with the protozoan species *Trypanosoma cruzi*, for example, the overall genetic variability of the species *C. albicans* is at least four times lower (M. Tibayrenc, pers. commun.).

Concluding remarks: many or no species concepts?

Providing a general and satisfactory species definition appears to be a very difficult task, especially given the very large number of potential applications

with different functional requirements (taxonomy, conservation biology, functional ecology, evolutionary biology and medicine). In fact, we do not believe that it is possible to reach a species definition that will satisfy everybody. In this paper, our aim is not to provide a new species definition because we feel the extant ones (typological, BSC, etc.) will continue to work in their different domains of application. Our goal is to draw attention to the fact that the most currently used concept (the BSC) might not be very helpful in parasitology, because of the reasons outlined above, and that it may prevent researchers from considering several evolutionary processes. The strong potential for diversification displayed by parasites, possibly due to the larger opportunities for sympatric speciation in such groups, should allow parasitologists to play a major role in different fields of biology. In evolutionary biology, parasites appear as ideal models for the study of specialization and speciation and much can be learned from them. In phylogenetic studies the genetic consequences of such potential for diversification should allow different hypotheses, such as the molecular clock, to be tested, in particular in groups where such a diversification is evident (eg. monogeneans and bird lice). Too few such studies are available at the present time. Parasite communities should provide very useful models for studying the interaction between species, competition and exclusion and biological diversity maintenance, because the ecological niche of a parasite will often be easier to define (as it is concentrated in the host). In medicine, the mechanisms involved in parasite diversification (in the wide sense) should allow a better understanding of eradication failures. Also, it should be considered more often that what appears to be a single pathogenic entity might actually comprise several very different genetic entities. As mentioned previously, the tremendous levels of genetic diversity found within *C. albicans* and *T. cruzi* reveal that these taxa are complex and surely made up of different biological entities (species). Because they co-exist, these different biological entities might have different ecological niches (ie. needs) and thus different sensitivities to one or another treatment.

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