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To Fuse or Not to Fuse? An Evolutionary View of Self-Recognition Systems

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Abstract

Self-recognition systems preventing chimera formation following somatic fusion between members of the same species have evolved only in certain phyla (e.g., fungi, cnidarians, poriferans, bryozoans, urochordates). We present here some of the biological features common to fungi and colonial marine invertebrates, which may have driven the evolution of such self-recognition systems. We conclude that the evolution of self-recognition mechanisms in fusible organisms is more likely to result from a complex trade-off between selection pressures linked with a gregariousness and sessile way of life. This trade-off also raises the question of how extrinsic interactions between a group of cooperative cells and its direct environment may have driven the evolution towards a form of individuality, via the emergence self-recognition systems in fusible organisms. Gregariousness and sessility being two features intrinsically associated emergence of multicellularity, somatic incompatibility systems could then be considered as one of the first expressions of individuality in early multicellular organisms.

Keywords: Somatic fusion; Fungi; Colonial marine organisms; Gregarious; Sessile; Coloniality; Individuality; Evolution; Chimera; Somatic incompatibility; Vegetative incompatibility; Self recognition; Individual

Introduction

Somatic fusion between the soma of two independent conspecific multicellular organisms is a mechanism observed in all major multicellular eukaryotic taxa (Figure 1). This ability challenges the concept of the individual as the unit for selection [1]. By contrast, self/non self recognition (SNSR) systems, preventing chimera formation between self but genetically unrelated members of the same species, has only evolved in fungi [2-4] and colonial marine invertebrates, such as poriferans, cnidarians, urochordates and bryozoans [5,6] (Figure 1). These systems have often been compared to the Major Histocompatibility Complex (MHC) of vertebrates, or the hybrid necrosis observed in several flowering plants [4,7,8].

Interestingly, fungi and colonial marine invertebrates have some other major ecological and biological attributes in common. They have: i) a similar mode of development, based on somatic embryogenesis [1,9], ii) a life cycle in which vegetative propagation is largely based on clonal reproduction or vegetative budding is common [4,10-12] and iii) a gregarious and sessile lifestyle resulting in intense competition for space and resources between individuals living on the same substrate [13-15]. Another shared characteristic is the intensity of the rejection reaction that can occur when individuals with incompatible combinations of alleles at recognition loci come into contact. In fungi, somatic incompatibility triggers several cellular changes, compartmentalization and cell death [16,17]. In colonial marine invertebrates, contacts between incompatible individuals may result in aggressive reactions, including inflammatory reactions, cell death and local tissue destruction [5].

Moreover, like other SNSR systems, such as the MHC or the plants hybrid necrosis [18], the allorecognition system of marine invertebrates and the somatic incompatibility system of fungi display high levels of recognition gene polymorphisms [3,5,19]. Several studies have investigated the evolutionary forces driving these polymorphisms on one hand, and the underlying reasons for the maintenance of somatic fusion in these taxa on the other hand [5,20-23]. Although similarities between the allorecognition system of marine invertebrates and the

somatic incompatibility system of fungi have long been emphasized [4,5,9], the hypothesis that similar forces were behind the evolution of these SNSR systems has seldom been thoroughly considered, with fewer studies considering both clades simultaneously.

Our first aim is to question the possibility of similar selective

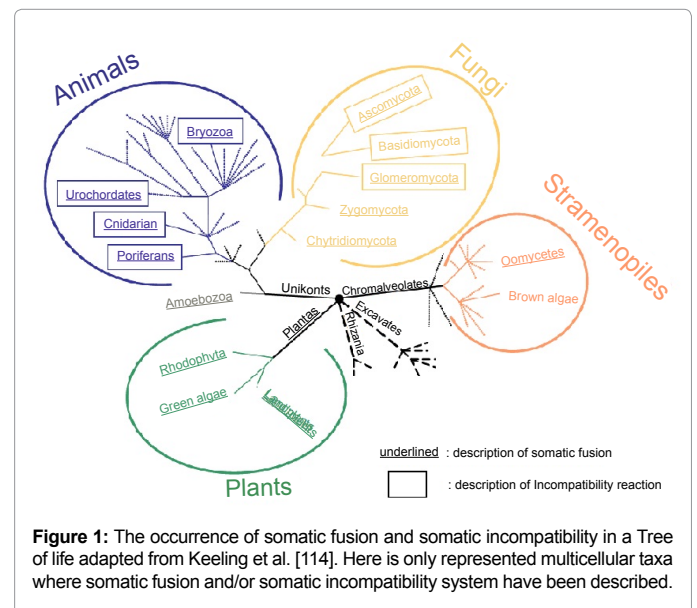


Figure 1: The occurrence of somatic fusion and somatic incompatibility in a Tree of life adapted from Keeling et al. [114]. Here is only represented multicellular taxa where somatic fusion and/or somatic incompatibility system have been described.

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pressures being the cause of a convergent evolution of SNSR systems in colonial marine organisms and in fungi. After a description, with a few examples, of the mechanisms characterizing these SNSR systems, this paper will review some key common features, as well as some phylum specific features that are potentially responsible for fusion/non-fusion behavior in fungi and/or colonial marine invertebrates. Furthermore, as stipulated by some authors [1,2], the question of the evolution of a SNSR system cannot be completely dissociated from the question of the evolution of individuality in fungi and colonial marine invertebrates. The definition of the individual, as a unit of selection, is well suited for organisms like vertebrates or arthropods for which the boundaries of such a unit are well defined. On the other hand, the fact that fungi and colonial marine invertebrates can fuse with conspecifics represents, among other features like clonality, a major issue for the delimitation of the somatic boundaries of an individual and for its genetic integrity [4]. The second aim of this work is then to highlight the role of SNSR systems which, by limiting somatic fusion to fusion with closely related conspecifics, allow the identification of a form of individuality in fusible organisms [1,2]. From this highlighting, an original point of view on individual evolution in fusible organisms is presented, considering the evolution of self recognition as the first step for the emergence of a convergent form of individuality in these taxa. We also discuss the possibility for broadening this idea to the first form of multicellular organisms and its consequences for the concept of individuality evolution in general.

Polymorphism of SNSR Systems in Fungi and Marine Invertebrates

Fungi

The determinism of vegetative incompatibility has been elucidated in a larger number of ascomycetes than of basidiomycetes [24]. In several basidiomycetes, genetic studies are hampered by the dikaryotic or diploid state and by the difficulty of obtaining fruiting bodies or germinating spores. Moreover, many ascomycetes are plant or animal pathogens and have therefore been studied in more detail with the aim of limiting their deleterious effects on their host and environment [25]. In basidiomycetes, vegetative compatibility is under the control of one or a few genes, called *het* or *vic* genes (heterokaryon or vegetative incompatibility genes). For example, at least one multiallelic gene is involved in *Phellinus weirii* [26], two genes in *Amylostereum areolatum* and *Serpula lacrymans* [27,28] and three or four in *Heterobasidion annosum* [29]. In ascomycetes, somatic incompatibility systems are characterized by a larger number of *vic/het* genes (frequently a dozen), with a limited number of alleles (often two but cases with three and more have also been reported) [17]. Some of these genes have been isolated and cloned in *Neurospora crassa* and *Podospora anserina*. Despite the close phylogenetic relationship between these two species, *N. crassa* and *P. anserina* present different *het* genes, suggesting that somatic incompatibility systems have evolved independently several times in fungi [17]. Traces of balancing selection in somatic incompatibility genes of species within *Neurospora* and related genera [30] and a signature of positive selection in the *het* genes of *P. anserina* [31] have also confirmed the hypothetical role of positive diversifying selection in the evolution of high levels of allelic polymorphism in the *vic/het* genes of fungi. Moreover, in two *het* genes of *P. anserina*, allorecognition specificity was found to be determined by a polymorphic WD repeat domain, characteristic of a large gene family (the HNWD family) [32]. The ten members of this family display strong architectural convergence with the highly polymorphic molecules of vertebrate and plant SNSR systems [7]. The existence of a hypermutation process,

allowing the propagation of a mutation acquired at any site within the WD-repeat domain between these *het* genes and any other locus of the same family, has recently been proposed by Paoletti et al. [31]. This concerted evolution between HNWD genes may contribute to the high levels of polymorphism and plasticity of this gene family in *P. anserina* [31]. Nevertheless, studies of the *vic/het* genes of additional fungal species are required to elucidate the mechanisms underlying this diversity. There is also still a lack of field studies to provide estimates of *het* gene polymorphism in wild fungal populations, which is almost certainly underestimated. For example, the number of biallelic *vic* loci in *Cryphonectria parasitica* (an ascomycete responsible for the chestnut blight disease) was initially estimated at six in Italian and Swiss populations [32]. However, population studies suggested that there was a larger number of *vic* loci or alleles in France [33,34] and especially in Asia, where *C. parasitica* has originated [35]. In the sampled Asian populations, 125 of the 143 isolates studied presented a unique combination of alleles at the *vic* loci, showing the potentially high diversity of *vic/het* genes in the field [36].

Colonial marine invertebrates

The genetic and molecular determinism of allorecognition mechanisms in marine invertebrates has been most widely studied in three species: the cnidarian *Hydractinia symbiolongicarpus* [37,38], the ascidians *Botryllus schlosseri* [8,39] and in the solitary ascidian *Ciona intestinalis* [40]. As in basidiomycetes, the incompatibility systems of these diploid organisms seem to be driven by a small number of highly polymorphic genes (one gene in most cases, [37,41]). To fuse, individuals have to share the same allele at these loci. High levels of polymorphism have been observed in natural populations [42,43]. The allelic diversity of three populations of *B. schlosseri* from the Israeli coast was studied by Rinkevich et al. [43], who found up to 306 different alleles of a locus controlling fusion outcome in a single population (*Fu/Hc* locus for Fusibility/Histocompatibility locus). Strikingly, no fusion between individuals from different sites 12 to 36 km apart was observed, suggesting that each allele was specific to a population. In a sample of 30 individuals of *B. schlosseri* from the Californian coast, Nyholm et al. [44] found 21 different alleles for the *fester* locus, which is also thought to be involved in the allorecognition mechanism of this species. They also showed that the non synonymous/synonymous substitution ratio was high for *fester* alleles, suggesting the occurrence of disruptive selection. More evidence for selection acting on *Fu/Hc* and *fester* in *B. schlosseri*, or on *alr2*, an allodeterminant of the colonial hydroid *H. symbiolongicarpus*, have also been recently found [38,41,45]. All these works suggest that the polymorphism of genes controlling the fusion outcome in colonial marine invertebrates is, like in fungi, a highly dynamic phenomenon which may be similar in diversity to the MHC system of vertebrates [8,38,43,46].

Not to Fuse: The Dangerous Drawbacks of Somatic Fusion

The risks of somatic fusions shared by fungi and colonial marine invertebrates

Germ-line competition: As pointed out by Aanen et al. [23], somatic fusion results in the soma being a “public good” and the different germ lines of the chimera compete strongly for control of this entity. This competition is particularly severe in fungi and colonial marine invertebrates, because of their mode of development based on somatic embryogenesis [1,9]. Throughout the life of these organisms, propagules are continually produced through hyphal or stem cell differentiation. These fusible organisms run a perpetual risk of post-

fusion invasion by different genomes likely to make use of conspecific somatic structure for the dissemination of their genes. For example, in the colonial ascidian *B. schlosseri*, fusion between genetically different colonies results in a hierarchical organization of the two germ lines of the newly formed chimera, potentially leading to replacement of the somatic and germ cells of the “losing” germ line by those of the “winning” germ line [47]. Laird et al. [48] studied the mechanisms of this case of germ-line competition in detail by transferring a single “winner” stem cell into somatically compatible and incompatible “loser” colonies via a colony-wide vascular network. They reported the contamination of propagule production by the genome of the transferred stem cells in three of ten cases for histocompatible colonies and not at all for incompatible colonies. They suggested that this situation resulted from competition between stem cells within the colony for access to the nascent gonads and the blastogenic buds, which appear to be important niches for the spread of the genome of each fused organism within the chimera. This highlights both the risk of germline invasion linked to somatic fusion and the key role of SNSR systems in maintaining the genotypic identities of the germ and somatic cell lines of fusible organisms. A nuclear exchange after fusion, which has also been described in sponges [49], is a well-documented phenomenon in fungi [50-55]. For instance, Debets and Griffiths [56] observed in *N. crassa*, the expression of two phenotypes, instead of only the mutant one, in the fruiting structures of a mutant mycelium, which had been in contact with asexual spores of a the wild-type phenotype.

Horizontal pathogen transmission: Somatic fusion allows the transmission of cytoplasmic elements, which are thought to exert selection pressure on SNSR systems [57-60]. In fungi, such cytoplasmic agents are even thought to induce the maintenance of a higher level of polymorphism for SNSR system genes than for parasitic genes [58]. Viruses infect many fungi, but only a few of these viruses are highly virulent in their fungal hosts [61-63]. These virulent viruses include Cryphonectria Hypovirus 1 (or CHV1), an RNA virus infecting *C. parasitica*, which has been studied extensively due to its use as a biological control agent for chestnut blight [64]. Like all known mycoviruses, CHV1 has no extracellular phase and hyphal fusions provide it with its only opportunity for horizontal transmission. Such transmission may occur between different vegetatively compatible types, but the frequency of transmission decreases with increasing vc type dissimilarity (vc for vegetative compatibility) [65]. The prevalence of CHV1 is higher in European populations of *C. parasitica*, which have a low allelic diversity for *vic* genes, than in American populations, in which vc types are much more diverse [59]. Fungi may also encounter diverse parasitic cytoplasmic elements other than viruses. Many cases of deleterious mitochondria [66,67] and plasmids [68] have been described in fungi, particularly for *C. parasitica*, *N. crassa*, *N. intermedia*, *P. anserina*, *Aspergillus amstelodami* and *Ophiostoma novo-ulmi*. The ecological and epidemiological characteristics of these deleterious cytoplasmic elements are poorly understood, due to a lack of field studies of the type conducted by Hoegger et al. [69]. These authors monitored viral and mitochondrial dispersion from a strain of *C. parasitica* released in the field. Within two years, the introduced viral and mitochondrial genomes had spread independently to the resident host fungus population. Fungi are thus continually at risk of becoming infected with parasitic cytoplasmic elements. Such a risk may also exist for marine invertebrates, although no experimental evidence is currently available to confirm this.

Pleiotropic hypothesis: The risks represented by conspecific fusion cannot be the only driver of the allelic diversity of SNSR system genes [23,70]. Polymorphism may also be an indirect consequence

of selection pressures acting on functions other than SNSR. For example, in *P. anserina* and *N. crassa*, the properties of vegetative incompatibility genes suggest that they have other cellular functions [70]. This implies that genes interacting during recognition may also be involved in the intrinsic fitness of the organisms and that selection fixes specific loci in each subpopulation. The *mat* locus of *N. crassa*, which controls the outcome of somatic fusion with conspecifics, is also the mating type locus regulating the choice of a mating partner. This highlights the potentially pleiotropic function of *het/vic* genes. Moreover, Paoletti and Saupé [7] hypothesized that pathogen recognition is the primary function of fungal incompatibility, with fungal SNSR systems resulting from the inappropriate activation of the pathogen recognition system in absence of any pathogens. This hypothesis is supported by the functional similarities of the proteins encoded by *het* genes in fungi, those encoded by genes involved in plant or animal responses to pathogen attacks [7] and by the fact that some bacteria may induce incompatibility reaction in *N. crassa* [71]. Interestingly, a similar case of pleiotropy in the MHC system has represented a serious bias for the understanding of its function, which was supposed to consist of graft rejection between individuals before finding its role in pathogen-recognition [7]. Allorecognition systems of colonial marine invertebrates are suspected to be the ancestral form of the vertebrates MHC systems [8,43,46]. Although such suspicions have now been disproved, it still could be hypothesized that allorecognition systems are associated with the control of an immune response in colonial marine invertebrates. Even if confirmed, this hypothetical pleiotropy would not eliminate the risks and benefits of fusion for the fusible organisms described in this review. However, the possibility of pleiotropic effects on the genes belonging to the somatic incompatible systems may complicate the detection of a clear signature of balancing selection in natural populations [59].

Specific to fungi

Genetic conflict: the occurrence of horizontal transmission of organelles during somatic fusions can represent a risk for genetic conflict between nuclear and cytoplasmic genomes. The syncytic state of filamentous fungi (i.e. no or weak delimitation between cells), combined with the occurrence of cytoplasmic exchanges during somatic fusion, may be responsible for the independence of cytoplasmic DNA from the nuclear genome [66]. This independence has been clearly illustrated by the study of Hoegger et al. [69], where a mtDNA has been found to have migrated to the fungal population independently from the introduced viral genome. Moreover, mitochondrial migration after fusion has repeatedly been reported in fungi [52,53,72,73], and the replacement of resident mitochondria by migrant mitochondria has also been described in *N. tetrasperma* [54]. As a consequence, in fungi more than in any other eukaryote phylum, a genetic conflict between cytoplasmic DNA and the nuclear genome, promoting the evolution of selfish organelles, is likely to exist. The report of several cases of deleterious mitochondria in fungi supports this hypothesis [66,67,74]. Interestingly, differences in size have been reported between the animal and fungal mitochondrial DNA (mtDNA) genomes [75]. Regular cytoplasmic exchanges following fusion in fungi and the high rate of mtDNA recombination [75], may account for fungal mtDNA never having reached the same degree of genome erosion as animal mtDNA [76]. The risk for genetic conflicts between cytoplasmic and nuclear genomes is generally seen as a major selective pressure in eukaryotes, responsible for the evolution of the uniparental inheritance of mtDNA ubiquitously found in fungi, plants and animals [77,78]. It could then be argued that the long-term benefits linked with the limitation of genetic conflict via the control of the horizontal transmission of

cytoplasmic DNA, has also been a motor for the evolution of somatic incompatibility systems in fungi.

To Fuse: The Evolutionary Benefits of Fusion

Evidence in both fungi and colonial marine invertebrates

The evolutionary benefits of fusion with self: Unlike motile organisms, fungi and colonial marine invertebrates cannot move when the environment 238 around them becomes detrimental. The foraging capacities of these sessile organisms therefore depend on their ability to exploit their direct environment to maximize the surface of the soma where exchanges can occur between substrate and organism boundaries [4,6]. By allowing the achievement of closely woven three-dimensional somatic structures, somatic fusions within the same organism increase the area over which exchanges can occur between substrate and organism. In this context, fusion with self would consist of an intrinsic mechanism during the development of those sessile organisms, allowing better foraging capacities but also bringing support for growth and homeostasis [79]. In a recent experimental study, Richard et al. [80] looked at the advantage of somatic fusions between clonal spores of the fungus *N. crassa*. They compared the effect of initial spore density on the growth of wild-type strains and a fusion mutant strain that cannot fuse. At high spore densities, wild-types colonies grew significantly larger than mutant colonies, providing evidence of fitness benefits associated with somatic fusion. Because Richard et al. [80] used clonal asexual spores, their result give some credit to the argument by Aanen et al. [23], stating that somatic fusion may be beneficial only when an individual fuses with itself. For this reason, SNSR systems would only allow fusion with self and, as a consequence, chimeras would represent rarities [81].

The evolutionary benefits of fusion with non self: The recurrent observations of bypasses of the barrier of incompatibility by juvenile stages in fungi and in colonial marine invertebrates challenge the point of view of Aanen et al. [23]. Indeed, specialized hyphae called conidial anastomosis tubes have been described in germinating spores of fungi species. These structures are able to form a stable fusion with other young mycelia regardless of the compatibility profile [82,83]. Similarly, several examples of ontogenetic changes in compatibility for colonial marine invertebrates exist in the literature [84-90], suggesting that fusion with non-self can be beneficial at an early stage in the development of colonial marine organisms. For instance, larvae of the sponge *Haliclona sp.* were found to be able to fuse with non-siblings, whereas adults fuse preferentially with self [91]. A higher acceptance rate of fusion between pairs of sibling colonies in freshly established colonies than in mature colonies was also found in the hydrozoan *Hydractinia symbiolongicarpus* [92].

These ontogenic changes in compatibility are likely to be the consequence of a strong size-dependent selection acting on sessile and gregarious organisms, like fungi and colonial marine invertebrates, especially during the early stages of life [2,5,9,92]. Such positive relationships between size and age in maturity and fecundity rates have been reported in some lichenised fungi and corals [93-96] but see [97]. In this context, somatic fusion could represent a benefit like those suggested by the reports of an increase in fitness following somatic fusion in some fungi or colonial marine invertebrates species [98-100]. Interestingly, Amar et al. [100] found while studying 544 colonies of a coral species over a period of one year, that growth and survival rates were higher for colonies generated by the fusion of several germ lines, whereas single-germ line colonies had the lowest survival rates. In the colonial ascidian *B. schlosseri*, Carpentier et al. [101] observed that

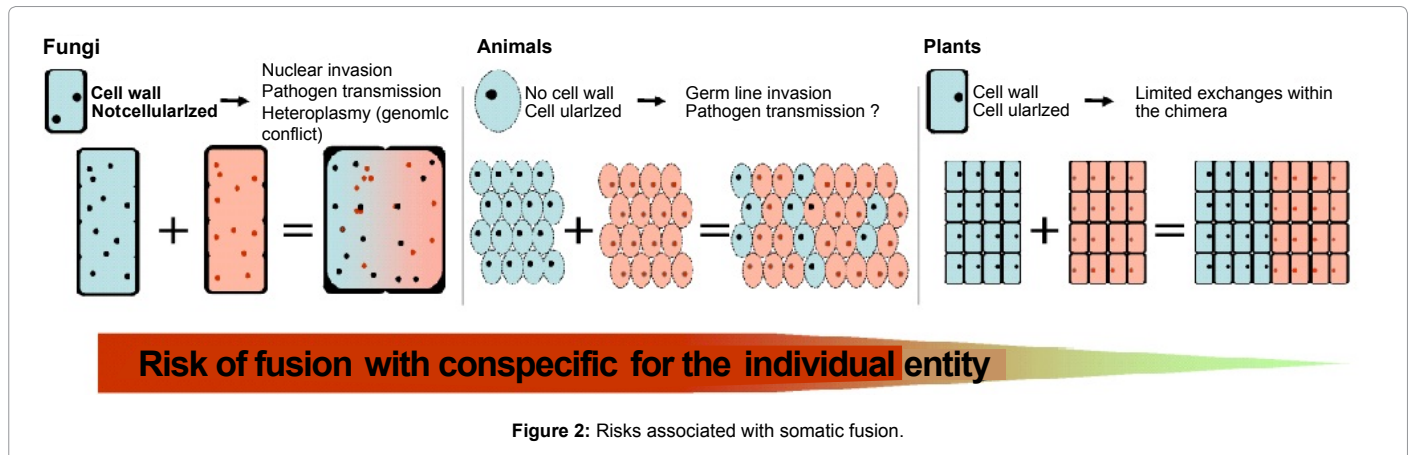
chimeras showed a higher fitness than non-chimeras at high-density growth conditions. This evidence, coupled with the observations of heterokaryons (i.e., fungi in which genetically different nuclei coexist in a common cytoplasmic) in natural fungal populations [102-105] highlight the major role of somatic fusion and chimera formation in the biology and ecology of both fungi and colonial marine invertebrates, a role that should not be underestimated.

Specific to Fungi

Heterokaryosis, parasexuality and horizontal gene transfer: One consequence of the syncytic state of filamentous fungi is that somatic fusions may result in a chimera in which genetically different nuclei coexist in a common cytoplasmic unit. It remains unclear whether these chimeras, which for fungi are called heterokaryons, are stable or transient in wild populations [106]. However, in both cases somatic fusion appears to be the principal force for maintaining the diversity of nuclei within the fungal mycelium, or for facilitating genetic exchange and recombination between asexual lineages. As previously mentioned, evidence for the existence of heterokaryons in wild isolates have been obtained for *C. parasitica* [103,105], *Plasmopara halstedii* [104] and other fungal species [102]. The coexistence, within the same cytoplasm, of different nuclei, is thought to result in somatic recombination with mitotic crossing over and independent assortment of chromosomes within heterokaryotic organisms. This phenomenon of parasexuality was described as early as 1953 in fungi [107] and is thought to be a major source of recombination in fungi, particularly in species with no known sexual structures [11]. However, the importance of genetic exchange during somatic fusion for the ecology and evolution of wild fungal populations remains poorly understood, due to the lack of data. Hyphal fusion and genetic exchange have been proposed as mechanisms accounting for the multigenomic nature and widespread occurrence of the arbuscular mycorrhizal fungi (*Glomeromycota*), ancient asexual fungi of considerable ecological and economic importance [108-110]. Evidence has recently been obtained to suggest that connections between genetically different isolates may be accompanied by heterokaryosis, genetic exchange and recombination in *Glomus intraradices* [111]. Horizontal gene transfer between members of the same species may drive evolutionary changes in fungi. The transfer of supernumerary chromosomes, which can be transferred across vegetative barriers [112], may be a key element in the evolution of soil-dwelling fungi, playing a role similar to that of plasmid transfer in bacteria [113]. Another example is provided by the genes that confer wilting in tomato, which have been shown to spread between clonal lineages of *Fusarium oxysporum* by horizontal gene transfer [114]. Interspecific gene transfers between related species have also provided indirect evidence for such transfers [115]. The emergence of a new disease on wheat might, for instance, be a direct consequence of the transfer of a virulence gene between two pathogenic fungi [116].

Somatic Incompatibility, Multicellularity and the Concept of Individuality

Some evidence for antagonist forces occurring in both filamentous fungi and colonial marine invertebrates are reviewed here. However, as previously stated by Buss [9], it would be naive to think that the allelic diversity of the loci involved in self/non-self recognition in fungi and colonial marine invertebrates results from a unique and well defined selection pressure. The evolution of SNSR systems in these organisms is likely to result from a trade-off between a complex network of selection pressures. The originality of this present work highlights that most risks and benefits connected to somatic fusions with conspecifics in fungi and colonial marine invertebrates are direct or indirect consequences



of a gregarious and sessile life style. Interestingly, plants are other gregarious and sessile organisms and fusion has been reported, in red algae [117] and also in higher plants [118]. Buss [1] suggested that because of differences in cellular organization, the risks associated with somatic fusion are not the same for fungi, animals and plants (Figure 2). In plants, because each cell is isolated by a rigid cell wall which limits cell mobility, the cost associated with somatic fusion is suspected to be negligible.

As stated in the introduction, the evolution of SNSR systems in fungi and colonial marine organisms has previously been presented as the expression of a form of individuality [1,2]. Studying the forces acting for the evolution of SNSR systems in these organisms provides an opportunity to think about the forces responsible for the evolution of a convergent form of individuality in fungi and colonial marine organisms. Interestingly, none of these forces appear to be relevant to the classical Weissmanian doctrine of separation of germ line and soma [1], which is still viewed by some authors as a key step in the evolution of individuality for multicellular organisms. For instance, Michod [119] sees the evolution of individuality to be based on an ancestral trade-off between survival and reproduction in unicellular organisms, which would have resulted, during the transition to multicellularity, in the specialization of cells into germ line and soma within a given entity. This present work shows that there might exist another route towards the emergence of a form of individuality, via SNSR systems, for species showing no sequestration, or a late sequestration, between germ and somatic lines. Indeed, for Buss [1], individuality evolution in animals results from an organized competition, between different cell lineages, during embryogenesis following the unicellular phase (i.e., zygotic phase) in multicellular life cycles. The evolution of an early separation between germ line and soma would then have been a first step in the evolution of individuality and would have concerned a limited number of taxa only, such as vertebrates or arthropods. However, this hypothesis cannot account for fungi as they do not present embryogenesis in their development. Interestingly, the study of SNSR systems in fungi and colonial marine invertebrates may suggest a third hypothesis that would be consistent with the biology of both phyla. This hypothesis is that risks linked with gregariousness and sessility, as described earlier in this review, may have driven the evolution of a form of individuality in these fusible organisms via the ability to recognize self from non-self. The originality of this alternative hypothesis is the suggestion of evolution of individuality is the result of extrinsic interactions between a group of cells from the same germ line and its direct biotic environment, and not as classically viewed [1], the consequence of cellular interactions within a group of cells.

Gregariousness and sessility are two features intrinsically associated with coloniality that has been a global trend in the emergence of multicellular organisms [1,120,121]. In consequence, similar altruistic and selfish interactions between groups of various degrees of relatedness, as described in this review, were likely to occur between colonies of the first forms of multicellular organisms. It may then be argued that the evolution of SNSR systems has consisted of the first expression of individuality in multicellular eukaryotes following the unicellular-to-multicellular transition. Other mechanisms thought to be at the base of the unicellular-to-multicellular transition [121], such as germline sequestration, maternal control over early embryonic development, or clonal development from a unicellular zygote in life cycles, would have been secondary steps toward the reinforcement of the individual as the unit subjected to selection during the evolution of multicellular eukaryotes [122]. At the same time, the evolution of nervous systems and motility would have reduced the occurrence of somatic fusions in some multicellular taxa. It could then be hypothesized that SNSR systems in those taxa would have evolved toward other functions than the control of somatic fusions, such as protection against mosaicism or pathogens recognition [81].

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