

Chimeras in Colonial Invertebrates: A Synergistic Symbiosis or Somatic- and Germ-Cell Parasitism?

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Abstract

Many colonial invertebrates settle and grow beside conspecific individuals. As a result tissues of different individuals come frequently into direct contact with each other. Self/non-self recognition mechanisms are known in a number of colonial animals from different phyla including sponges, cnidarians, bryozoans and tunicates. These mechanisms control rejection or fusion of adjacent tissues that come into contact with each other. Many studies have documented the existence of naturally occurring chimeras in these phyla and it has been proposed that several types of ecological and biological benefits accrued to these chimeric colonies. The present paper summarizes past results from field and laboratory studies on the outcomes of natural conspecific-fusions in a reef branching coral *Stylophora pistillata* (Cnidaria) and a colonial tunicate *Botryllus schlosseri* (Protochordata). These two species represent two different types of natural chimeras, sectorial and cytotoxic (mixed cell) chimeras, respectively.

In a fused pair of corals, photosynthetic metabolites are translocated from the "inferior" colony to the "superior" one, which utilizes these products for its metabolic requirements. A significant decline in both somatic and germinal development usually results. After a long period of fusion one of the partners in the chimera (usually the subordinate) dies. Similarly, after somatic fusion in *Botryllus* colonies, a complete resorption of one of the chimera is often the result. Death of one of the fused colonies often subsequently led to the death of the other colony. In some cases eggs of one colony were transferred and brooded within the developed zooids of the second colony of the pair.

We suggest that chimerism in invertebrates may present substantial fitness costs, and involves an array of competitive interactions between the two partners. These include cell lineage competitions and competition for energy resources. If the alternate suggestion is that chimeras between closely related organisms is advantageous, such chimeras should be abundant in nature. This is not yet documented. We therefore propose that chimerism in the invertebrates is characterized by somatic and germ cell parasitism rather than synergistic symbiosis and other benefits.

Keywords: chimera, colonial invertebrates, corals, natural chimera, somatic- and germ-cell parasitism, symbiosis, Tunicata

1. Introduction

A chimera (latin: chimaera=monster) is an organism containing tissues derived from at least two genetically distinct organisms. A chimera can be a whole organism, however, many experiments reported in the literature deal with separate organs or cells of a chimeric structure, a situation which had been designated as "graft-symbiosis" (by Buder, 1911; cited in Issayev, 1924). A chimeric stage offers an avenue of exceptional value for studying development, genetics, physiology and behavior as well as model systems for testing theories of immunology, and is used experimentally in an array of organizational arrangements from the whole organismic level (e.g., Issayev, 1924; Hauenschild, 1954, 1956; Lee and Campbell, 1979; and literature cited) to the cellular and molecular biology levels (e.g., West, 1978; Weissman et al., 1978; Blanden et al., 1981; Wanek, 1983; and literature cited). In most of these studies chimerism is used to reveal developmental and/or functional properties of the tissues or cell of different individuals (sometimes of different species), by the formation of a type of chimera which never takes place in these species in nature. We designate this type of chimera as an "experimental chimera". On the other hand, naturally-occurring chimeras are known to exist in other species including protists, plants and several groups of animals, distributed over at least 9 phyla (Buss, 1982). This type of chimera will be termed here as "natural chimera". Only natural chimeras will be discussed in the present paper.

Natural chimeras have been found in some cases to be significantly advantageous to the life history of the involved organisms. For example, high frequencies of sporeling (the early stages of a plant developing from a spore) coalescence in developing gametophytes and tetrasporophytes of red algae were recorded in several species. This was associated with an enhancement of blade initiation and frond growth compared to non-coalesced sporelings

(Tveter and Mathieson, 1976). These authors interpreted this chimera to be beneficial in competition for available substrate. Another ecological advantage was proposed by Jones (1956) who noticed that the habitat of the red alga *Gracilaria verrucosa* is exposed to sand scouring, a situation where frond growth enhancement would be beneficial. Similarly, Pilosa (1962; and literature therein) showed that mixed (i.e., heterocytosis) strains of cellular slime molds produced fruiting bodies of a more advanced development than either one of the strains alone. Although natural chimeras are also known in marine invertebrates (reviewed by Buss, 1982) very little is known about the possible benefits of chimerism to the interacting organisms. To our knowledge, only two studies (Buss, 1982; Grosberg and Quinn, 1986) discuss the consequences and the evolutionary significance of these chimeras. According to the studies, several sets of benefits might be attributed to chimeric individuals, as follows:

1. Since a natural chimera has a greater store of genetic variability and hence, wider ranges of physiological qualities and characteristics, chimeras may tolerate a greater range of environmental variation than genetically homogeneous organisms.
2. The two organisms may form a synergistic complement, in which two aberrant genotypes can produce normal structures when they form a chimera.
3. Since fusion leads to an immediate increase of body size, it may consequently increase survivorship in species where survivorship is size dependent.
4. When onset of reproduction is also size dependent, a chimera formed by two prereproductive organisms may result in a bigger organism of sufficient size for reproduction, thereby lowering the age of first reproduction.
5. Some ecological benefits: The consequences of the chimeric increment of the body size may be competitively advantageous to sedentary species which compete for any available substratum. In addition, this increase may neutralize the harmful effects of partial predation (resulting in prey injury) and may increase environment tolerance, such as to sand abrasion in shallow water (also Jones, 1956; Tveter and Mathieson, 1976; Sammarco, 1982).
6. Chimerism in sedentary organisms (which are incapable of controlling the timing and location for contacts with potential mates) may also ensure that mate location will not be a problem when necessary, i.e.,

as a result of environmental stress. This suggestion is limited to organisms in which sexually compatible individuals are also compatible in somatic tissue fusion.

It is important therefore to test directly the benefits and costs of chimerism in natural settings. In his discussion on the evolution of mechanisms of somatic tissue compatibility, Buss (1982) has suggested some potential costs of chimerism. For example, cell lineages within chimeric individuals may compete for limited resources. Although such competition may be adaptive, in other cases it can also be maladaptive. In addition, the occurrence of two genotypes within the same organism raises the possibility of competition between lineages for positions in the germ line. Since cell-lineage competition is clearly a potentially severe cost to the chimeric state, Buss (1982) suggested that this linkage limits chimera formation to closely related individuals. Although natural chimeras are recorded from several invertebrate phyla such as Porifera, Cnidaria and Tunicata (Buss, 1982), very little is known of the mechanisms or the consequences (benefits and costs) of chimerism. Here we discuss and examine results of two differential types of natural chimeras found in colonial marine invertebrates, the chimera of the hermatypic coral *Stylophora pistillata* from the Gulf of Eilat, Red Sea, and the chimera of the compound ascidian *Botryllus* from Monterey, California.

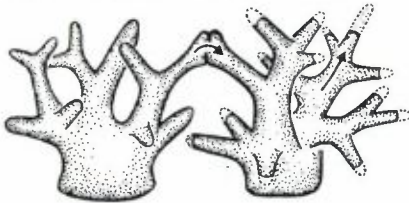
2. *Stylophora pistillata*

It is well documented that colonies of the same coral species which cosettle beside one another can subsequently fuse (Gardiner, 1931; Lang, 1973; Rinkevich and Loya, 1983a). Fusion between compatible broken fragments was also recorded in the field after storms, such as hurricanes (Gilmore and Hall, 1976; Tunnicliffe, 1981). A gregarious settlement and fusion of coral larvae likewise was recorded in all coral species so far examined for this (Goreau et al., 1981; Rinkevich and Loya, 1983a; Hidaka, 1985; Jackson, 1985, and literature therein). Fusion between distinct, sexually produced polyps to produce a bigger colony was designated as "aggregated colonies" (Koch, 1892), and is synonymous to our term of "natural chimera". Only in one case was it suggested that this type of fusion carried ecological benefits from the standpoint that the chimera allows the young colony to attain sufficient size to survive predation and/or competition (Sammarco, 1982). Nevertheless, the long-term consequences of fusion of primary polyps were rarely followed. However, Boschma (1929) did indicate that mortality of some of the fused newly settled *Maeandra* larvae within the chimera occurred 17 days after

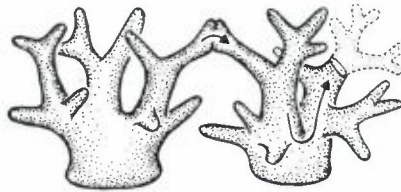
fusion, and Duerden (1902) did find that the growth of aggregated colonies were slower compared with that of isolated individuals.

Field observations and experiments were conducted on fused colonies of the Red Sea coral *Stylophora pistillata* (Rinkevich, 1982; Rinkevich and Loya, 1983a,b, 1985). These studies revealed several types of deleterious effects on at least one of the members in the chimera (Figs. 1, a-d; 2, a-b).

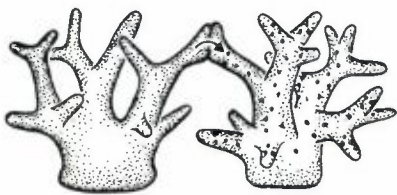
A. Translocation of Materials



B. Regeneration



C. Reproduction



D. Death



Figure 1. The consequences of a coral natural chimera (see text for further details).

S. pistillata (Esper) is one of the most abundant coral species in the Gulf of Eilat. It is widely spread in the lagoon, rear reef and reef flats, and abundant in the fore reef (Loya, 1972). This branching coral exhibits a wide variety of color morphs, from pale yellow to dark purple. Although the color morphs were not genetically determined, it was experimentally found that purple colonies were superior to the yellow morphs and competitively excluded them. This process is first characterized by a point of rejection on the histoincompatible tissues. In some cases, however, fusion between different color morphs was observed in experimental field grafts as well as between branches of naturally cosettled colonies (Rinkevich and Loya, 1983a). Since the color morph of each partner in the chimera did not change after fusion and since the border line between the two colonies was constantly marked by

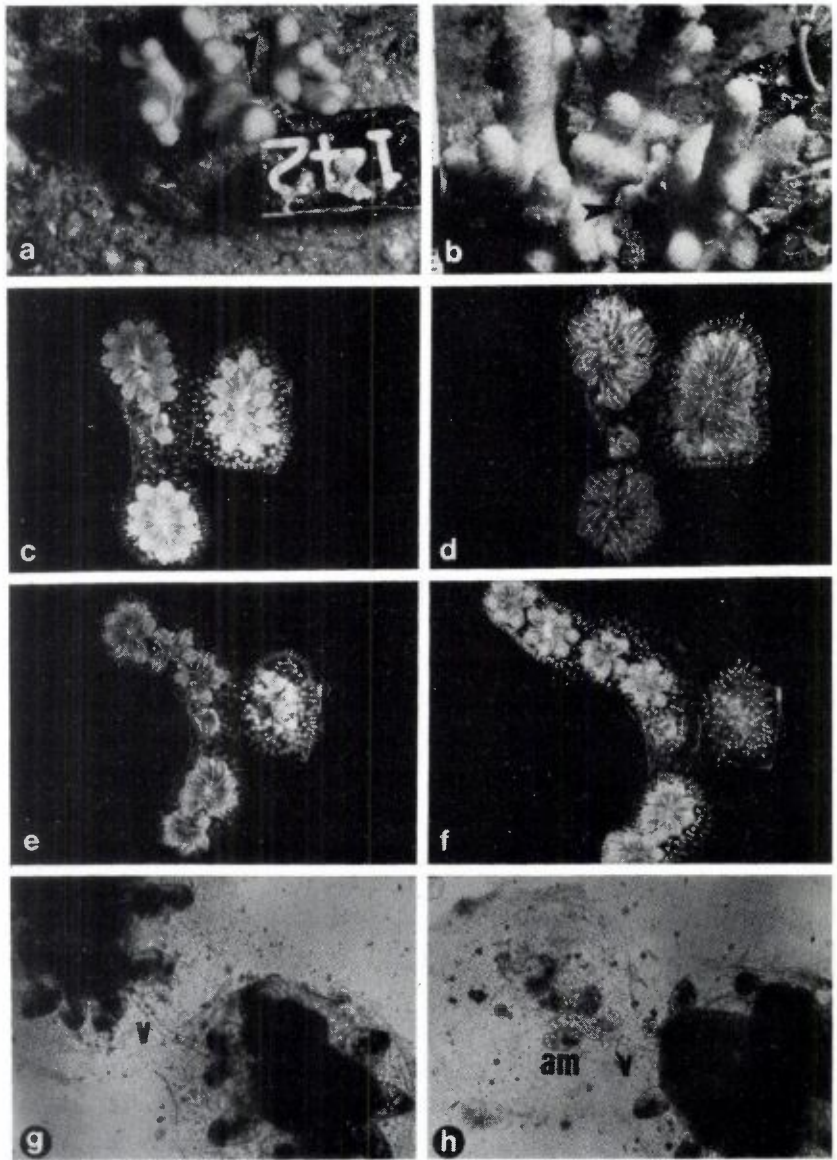


Figure 2. The consequences of natural chimeras in *Stylophora* (a-b) and *Botryllus* (c-h). a-b: A natural chimera formed by fusion between two basal plates of *S. pistillata* colonies. a=Immediately after fusion, b=13 months after fusion. The contact zone (marked by an arrowhead) "moved" on branches of the subordinate colony (left colony). c-f: *Botryllus*, resorption in large colonies; 5, 8, 16 and 22 days after fusion, respectively. The right colony is the subordinate. g-h: A resorption in *Botryllus* oozeoids, g=Fusion by one vessel (v), h=1 week later, resorption of the left oozeoid main body, ampullae (am) are still operating.

an irregular suture of tissue and skeleton, it was easy to follow the chimera *in situ* without any experimental interference. Some of the observations lasted more than 55 months. Once fusion was established, the tissue of the dominant partner in the chimera (usually matched with its color morph) eventually overgrew slowly the inferior partner's branches. In other cases, fusion between two adjacent colonies in the field developed through contacts in the basal plates of the colonies instead of branches. One of the basal plates overgrew the second, and with time, overgrew branches of the other colony as well (Fig. 2, a-b). The death of the inferior colonies in 11 natural chimeras and many additional experimental chimeras (schematically illustrated in Fig. 1d) occurred after a long period of overgrowth, up to 5 years (Rinkevich and Loya, 1983a).

In another set of experiments, chimeras were established by allografting branches which had been previously labeled with radioactive carbon ($\text{NaH}^{14}\text{CO}_3$) in the light. The ^{14}C -containing photosynthetic metabolites translocated from the labeled branches in an oriented pathway to one or two branch tips of the host, away from the fusion area. The recipient colony utilized these energy rich materials for its metabolic requirements (Fig. 1a). The $^{14}\text{CO}_2$ produced through respiration was consequently detected in the skeletal carbonate of the branch's tips as $\text{Ca}^{14}\text{CO}_3$. On the other hand, ^{14}C -labelled metabolites were not translocated from control isografts or from allograft branches of superior colonies grafted on yellow partners. This energy translocation, which by definition is a classic case of parasitism, was directed correspondently with the hierarchy of color morphs of the partners in the chimera (Rinkevich, 1982; Rinkevich and Loya, 1983a).

S. pistillata possesses the ability for rapid regeneration of broken branches. Within a colony, damaged branches grow faster than intact branches which results in a tendency to regain the symmetry lost through earlier breakage (Loya, 1976). Preliminary experiments (Ido, Loya and Rinkevich, unpublished) indicate that regenerated superior colonies which fused with radioactive-labeled branches from subordinate partners translocate the labelled photosynthates energy-rich materials from the subordinate partner toward the regenerating portions (Fig. 1b).

In addition, fusion between two compatible *S. pistillata* colonies decreased overall growth rate and reproductive output of the chimera (Rinkevich and Loya, 1985). Field experiments demonstrated a significant decline in the growth rate of fused colonies compared to the individual controls of the same size. This was recorded in the two members of the chimera, irrespec-

tive of their place in the hierarchy of the dominance. However, the subordinate colony was much more affected than the superior one. Moreover, the typical symmetrical shape of the interacting colonies, especially of the subordinate, changed to an abnormal growth form. The number of female gonads per polyp counted in histological sections was also significantly reduced, markedly in the subordinate genotype (Fig. 1c), in which the typical synchrony in reproduction among different branches within the colony was changed and desynchronized (Rinkevich and Loya, 1985).

3. *Botryllus*

Some colonial ascidians have the property of forming a natural parabiotic union (natural chimera) in the wild with other members of the same species, given that they share at least one allele at the histocompatibility locus (reviewed by Taneda et al., 1985). In the genus *Botryllus*, fusion between genetically distinct individuals is controlled by a single gene locus with multiple codominantly expressed alleles (Oka and Watanabe, 1960; Sabbadin, 1962; Scofield et al., 1982). A wild *Botryllus* colony is usually heterozygotic at this locus. Sibling larvae cosettle rapidly after their release resulting in a high probability of fusion between colonies (Grosberg, 1987). In addition, cosettlement of siblings sharing a histocompatibility allele has been reported to occur more frequently than that expected if larvae settle randomly (Grosberg, 1987; Grosberg and Quinn, 1986).

In botryllid ascidians fusion occurs between extracorporeal blood vessels (ampullae) of the two colonies. After the establishment of a common blood circulation, in which blood cells from the two partners are intermixed, this chimera may be termed as "cytomictical chimera" (sensu Issayev, 1924: a chimera in which the cellular elements of the two parent organisms have become so thoroughly mixed that they can no longer be separated into individuals). A complete mixture of blood-borne pigment-cells occurred within 4–14 days, and was marked as changes in the original color morph of both partners of the chimera (Rinkevich and Weissman, 1987a). A *Botryllus* chimera differs therefore from a coral chimera in which there is no evidence of mixed cellular elements and where each of the partners continues to possess its original color morph. The coral chimera is therefore a mosaic or sectorial chimera (sensu Goetsch, 1922). It should be noted here, that cytomictical chimeras were experimentally produced in other cnidarians belonging to the class Hydrozoa. Many of the hydroid's highly specialized cell types are part of a single lineage of cells that is continuously being renewed by proliferation

and differentiation of a stem cell called the interstitial cell. In experimental animals where the entire interstitial cell lineage is removed, an "epithelial" animal is left, which is composed only of ectodermal and endodermal epithelial cells. This animal can then be repopulated by interstitial cells taken from another strain or another species. A number of chimeric strains have been made in this fashion (for example, Lee and Campbell, 1979; Littlefield, 1984; and literature therein). However, this type of chimera strictly exists in experimentally manipulated chimeras, never recorded in any cnidarian in nature, and therefore cannot be regarded as "natural chimera."

Laboratory experiments on *Botryllus* chimeras (Fig. 2c-h) were performed on chimeras of both adult partners (Rinkevich and Weissman, 1987a), on chimeras of an adult and a young partner (Rinkevich and Weissman, 1987b) and chimeras of both partners of oozoids or young colonies (Scofield et al., 1982; our unpublished results). It was found that once a cytotoxic chimera was established (complete mixing of pigment cells is seen) one of the partners was often completely or partially resorbed. The resorption in large colonies started in zooids lying in closest proximity to the contact zone, while small colonies (of one system and less) or oozoids were resorbed at once. Several characteristics of the resorption were summarized as follows (Rinkevich and Weissman, 1987a,b):

1. *Botryllus* probably possesses gene system(s) which govern resorption. As a result, when similar-size pairs of subclones from colony A and colony B fused, subclones of only one of the two colonies (e.g., colony B) are resorbed.
2. Resorption can be a one-way process or a reciprocal phenomenon.
3. Genetic control of color phenotype is not linked to genetic elements controlling resorption.
4. The determination as to which colony will be resorbed in the chimera is also influenced by the relative body size of the two interacting colonies. Therefore, in some experiments a small subclone of a superior colony was resorbed after fusion to a large subclone of subordinate colony.
5. Resorption in large fused colonies is a slow process, lasting up to 8 months. In small fused colonies or oozoids it takes sometimes only 1 week.
6. Resorption of zooids usually proceeds during the "takeover" phase (the time when a new generation of asexually-derived zooids take over the colony from the previous generation) and does not include the blood vessels.

7. The resorption in *Botryllus* is probably controlled by two genetic loci, one which is linked to the fusibility/histocompatibility locus, and another which is not (Saito and Weissman, in preparation).

We also followed the fate of larvae of *Botryllus* that had cosettled with their parental colony (Rinkevich and Weissman, 1987b). Offspring share with their natal colony at least one allele at the histocompatibility locus (in addition to half of their genetic information), and therefore have the capacity to fuse with it. After fusion most of the fused offspring were resorbed. The few which survived were fused to parent colonies which degenerated or died. Not only survivorship, but also decreased growth rate occurred with progeny fused with the parental colony. In two cases of our study on fusion between offspring and adults, large eggs were found within the premature offspring's zooids, presumably translocated from the maternal colony through the connecting blood vessels. Germ cell exchange between fused *Botryllus* colonies has been recorded before (Sabbadin and Zaniolo, 1979). Sabbadin and Zaniolo (1979) fused colonies of different pigment genotypes for several days and thereafter separated them. Each of the colonies was then sexually crossed with another colony possessing recessive pigment alleles. By scoring the offspring pigment phenotypes, they showed that not only immature oocytes, but also undifferentiated germ cells were exchanged between the parabionts and then gradually matured as eggs or sperm in a prolonged series of generations (Sabbadin and Zaniolo, 1979). Thereafter, in some hatches of offspring from the fused colonies, the progeny were mostly or totally allogeneic (Sabbadin, 1982).

In other sets of experiments, we partly subcloned several large colonies of *Botryllus* and paired them with other subclones of histocompatible colonies (experimental subclones). These pairs of the experimental subclones fused and formed chimeras. The remaining parts of the large colonies were further subcloned (control subclones). Each of the control subclones which belonged to the same colony was put separately in a different experimental tank. One to three months later, all subclones which derived from some colonies (control subclones and experimental) underwent degeneration which led within 1 week to their death. The dying experimental subclones in the chimeras died together with their fused partners which derived from other *Botryllus* colonies. However, the controls of these second colonies continued to grow without any sign of degeneration or mortality. This result therefore demonstrates another deleterious consequence which occurs when forming a chimera with a degenerating or a dying colony.

4. Discussion

In this paper we focus on two natural chimeras, the sectorial chimera of the Red Sea coral *Stylophora pistillata* and the cytotoxic chimera of the compound ascidian *Botryllus schlosseri* from Monterey, California. The results obtained previously on these chimeras (Rinkevich and Loya, 1983a,b, 1985; Rinkevich and Weissman, 1987a,b) in addition to results obtained on botrylloids as well as other compound ascidians and cnidarians (in literature) are presented here to illustrate that natural fusion between different colonies may carry substantial fitness costs. Although naturally occurring chimeras were recorded from 4 different phyla of sedentary marine invertebrates (Porifera, Cnidaria, Tunicata, Bryozoa; reviewed in Buss, 1982, Jackson, 1985) there has been almost no data presented stating that the chimera stage is a disadvantage to at least one of the partners in the chimera. Even the work of Sabbadin and Zaniolo (1979), which demonstrated germ cells exchanged between different genotypes in the cytotoxic chimera of *Botryllus*, focused on the questions of sexual differentiation and maturation rather than in the ecological aspects of this phenomenon. Therefore, Sabbadin and Zaniolo (1979) did not study potential competition between the two germ lines. Only in lower organisms such as fungi, myxomycetes and cellular slime molds was it documented that after fusion of organisms of equivalent size and reproductive condition, one strain had successfully placed a disproportionate number of cells in reproductive cell lines (reviewed by Buss, 1982). While the question of the benefits of chimerism in higher organisms is still open, Buss (1982) in his general discussion on the benefits which are attributed to chimeric individuals, and Grosberg and Quinn (1986) in their discussion on colony fusion in *Botryllus*, suggested that colony fusion may be beneficial among kin. The two cases of natural chimeras which are discussed in the present paper, however, suggest that the chimera stage in colonial invertebrates is not beneficial over the long term to the involved partners. Instead of gains attributed to developmental synergism, a faster onset of reproduction, higher genetic variability and some ecological advantages (Jones, 1956; Tveter and Mathieson, 1976; Buss, 1982; Sammarco, 1982; Grosberg and Quinn, 1986) — the chimeric stage as it is presented from the studies on *Stylophora* and *Botryllus* is usually deleterious to at least one of the partners in the pair. Fusion between colonies of *B. schlosseri* is therefore not always beneficial, even among kin. Our results suggest the possibility of several noxious interactions, including competition for energy resources and cell lineage competition (germ-cell and somatic-cell parasitisms).

In natural chimeras of corals as is found in *S. pistillata*, cell lineage competition cannot be developed because of the lack of any evidence for mixture of cellular elements and hence, each one of the partners in this mosaic (or sectorial) chimera maintains its individuality. In the reef, interspecific competition for the substrate, a limited resource may be a substantial evolutionary selective force for the cosettlement of genotypically related coral larvae. Cosettlement resulted in the natural fusion of coral colonies. While it is not recorded yet in natural chimeras, cell lineage competitions were observed in many cases of experimental chimeras of the Cnidaria. For example, Campbell and Bibb (1970) summarized past experiments which dealt with long-term observations on hydrozoan experimental chimeras. In some of these experiments, newly formed buds had either regressed or degenerated, so that the tissue of one partner was eliminated (most of these studies were performed on chimeras of two different species). Noda (1970) presented another interesting case in which the nematocytes of one of the species in the chimera were incorporated into the tissue of the other species, in which the epidermal layer was sent into a state of "depression". Germ-cell parasitism was also recorded from several experimental chimeras of Hydrozoa, where one of the sexes dominated the other, i.e., a female animal became masculinized by the male partner, and vice versa (Campbell and Bibb, 1970; Littlefield, 1984 and literature therein cited). It should be noted, however, that the nature of this phenomenon is still circumstantial and the processes involved are yet unknown. Moreover, this phenomenon never takes place in nature.

The competitive interactions between cell lineages in the chimeric state of hermatypic corals are not yet understood. Even the genetic basis for these responses in corals is unknown (Willis and Ayre, 1985). Knowledge of the genetic basis for the phenomenon is important for the issue of cell lineage competitions and parasitism, since these phenomena could also be controlled with or related to gene systems which govern self/non-self discrimination. Basically, two different working hypotheses can be proposed to explain the results of "self/non-self recognition" in corals; in the first, fusion will occur only between individuals with identical genotypes, or alternatively, histocompatibility is determined by alleles at one or few loci (as in *Botryllus*, Scofield et al., 1982). Buss (1982) further suggested that somatic compatibility systems have evolved to preclude competition between cell lineages. However, until the genetic of the self/non-self recognition in corals is solved, any suggestion for evolutionary benefits in a coral chimera should be viewed with caution, at least on theoretical grounds, keeping in mind the results on

Stylophora.

In contrast, the genetics of self/non-self discrimination in *Botryllus* is well known and demonstrated by several independent investigators (Oka and Watanabe, 1960; Sabbadin, 1962; Scofield et al., 1982). In addition, a recent study has demonstrated that the resorption phenomenon is controlled by at least two genetic loci (Saito and Weissman, in preparation). Since *Botryllus* chimeras are a true case of cytotoxic chimeras, the co-occurrence of cells derived from two different genotypes within the same entity (the chimera) permits cell lineage competition. Moreover, our results indicate that fusion is usually a potentially severe cost to at least one of the partners. For example, if one of the colonies in the chimera just died, this will result in the death of the second colony in the pair, regardless of the relative positions of each partner in the cell lineage competitive hierarchy. Although we do not yet know the processes involved during resorption, it is evident that one of the competitors is physically eliminated. On the other hand, the phenomenon of germ-cell exchange between *Botryllus* colonies (Sabbadin and Zaniolo, 1979; Sabbadin, 1982; Rinkevich and Weissman, 1987b) raises another subject: Any genotype that is more effective in placing its germ line cells into a successful maturation should be at an evolutionary advantage, even if its somatic cells are eliminated during the process of resorption. *Botryllus* appears therefore to be an excellent invertebrate species in which functional intraspecific parasitism may be studied in detail.

Buss (1982) suggested that somatic compatibility has evolved to preclude possible competitions between cell lineages. In *Botryllus*, as a result of the nature of genetically-defined somatic tissue compatibility, fusion is possible only between closely related organisms or others which share at least one allele in common at the fusibility histocompatibility locus (Oka and Watanabe, 1960; Sabbadin, 1962; Scofield et al., 1982). This phenomenon eliminates fusion between different species or even between different individuals of the same species which do not share an allele in common at the histocompatibility locus. Furthermore, in *Botryllus* (as in other colonial invertebrates; Jackson, 1985) the larvae usually settle gregariously (Grosberg and Quinn, 1986; Grosberg, 1987), a phenomenon which increases the likelihood of fusion between compatible, kin colonies, above that expected if larvae settle randomly. We have presented here results which suggest that colony fusion may result in cell lineage competitions between genetically related colonies, in contrast to the suggestion (Buss, 1982) that cell lineage competition should be reduced in chimeras formed by closely related members. Perhaps relevant

to this discussion is the interesting naturally occurring cytotoxic chimeras, which has been found in the South American primates, *Saguinus oedipus* (cotton-top tamarins). These animals normally give birth to dizygotic twins which are bone marrow chimeras. This species is characterized also by an unusually high incidence of spontaneously occurring adenocarcinoma of the colon; and also frequently develops a fatal lymphoproliferative syndrome following infection with various herpes viruses. These diseases were linked by several investigators to the natural bone marrow chimerism (literature cited in Picus et al., 1985), which again, indicates some fitness costs to the chimera. If a chimera between closely related organisms is really advantageous to this entity when confronted with any selection pressure, one should be expected to find chimeras of two or multi-organisms in some frequencies in nature. This should be manifested by the gregariously cosettlement of many invertebrates larvae. However, as far as we know this situation is not documented and no available data supports this expectation in invertebrates. Therefore, it is proposed that some selective forces may be deleterious to long-term chimeras in nature, unless these chimera are cleared from mixture of genetically distinct cell lineages, by the processes of cell lineage competition. It is conceivable that chimera formation may be beneficial over the short-term (e.g., as in competition for suitable substrate, against other sedentary species), and that the resorption process, although certainly not beneficial to the resorbed individual, results in enhanced ability of the surviving individual to pass on traits inherent in the parent colony of conspecific, cosettling kin.

In conclusion, the results on *Stylophora* and *Botryllus* suggest that chimerism may over the long-term present substantial fitness costs. We suggest that the chimeric state of colonial invertebrates may involve an array of competitive interactions between the two partners. These include cell lineage competitions and competition for energy resources. It is proposed therefore that chimerism is characterized by somatic and germ cell parasitism rather than a synergistic symbiosis of evolutionary advantageous processes.

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