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THE BRANCHING CORAL *STYLOPHORA PISTILLATA*: CONTRIBUTION OF GENETICS IN SHAPING COLONY LANDSCAPE

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ABSTRACT

Colony architecture in branching colonial organisms is established through iterated processes of the structural units (modules), both zooids and the branches. Different approaches to analyzing colonial organization have revealed an intrinsic order to branched forms. By using mathematical models such as fractals, simulations of diffusion and flow, applying tree architectural models and developmental canalization ideas or analyzing heterochrony, attempts have been made to mimic the rules of colony formation. However, most approaches have not prioritized the rationale that structures and rules which govern the way a branching organism is built are heritable characteristics, and that even phenotypic plasticity is the expressed outcome of plasticity genes. There is no model system yet for the study of genetic impact on the architecture of branching modular organisms. *Stylophora pistillata*, an Indo-Pacific hermatypic coral, is treated here as such a model. *S. pistillata* morphometric characters are then analyzed. I raise the possibility that genetics is a key factor in shaping colony landscape and that genetic factors should be considered when studying the architecture of marine branching forms.

MODULES AND PLASTICITY

One of the central questions in developmental biology is the issue of how different species evolve different morphologies (Purugganan, 1998) and, within a given species, how conspecifics exhibit distinctive and diverse morphological features. The ability of organisms to produce different phenotypes under different environmental and biological challenges and conditions (a phenomenon termed "phenotypic plasticity") is one of the fundamental aspects of developmental biology. A number of studies in the past few years have demonstrated the existence of "plasticity genes" that specifically respond to a particular type of environmental alteration by triggering a given pattern of morphogenic change (Pigliucci, 1996).

Some species represent high phenotypic plasticity. However, even in such cases, there is also the possibility that a stringent species-specific "morphometric code" applies. Such a code is composed of a set of rules common to processes that are used

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repeatedly and in different combinations, to make living organisms functional under variable environmental conditions. In other words, the elements that construct an organism (animal, plant, etc.) are heritable characteristics of each species. One such example is the geometrical body invariance known as symmetry (Goldstein and Freeman, 1997; Levin, 1997; Martindale and Henry, 1998).

A variety of animals, mainly aquatic sedentary sessile organisms (sponges, corals, hydrozoas, bryozoans, tunicates) that are made up of modular units (usually called "polyps" or "zooids") cumulatively form structures termed "colonies". Colonies are therefore a tessellation of their structural modules. Colonial animal modules may vary significantly in size, architecture, arrangement in space, pattern, integration, and mode of development (Jackson and Coates, 1986; Tuomi and Vuorisalo, 1989; Pedersen and Tuomi, 1995). I accept the idea that a compound organism with colonial architecture does not represent an aggregate of individuals, but instead may be regarded as a single organism possessing characters of morphological and physiological integrity. This is based on Beklemishev's (1970) suggestion of the "balance" between a gradual increase in colonial individuality versus a simultaneous decrease in individuality of the zooids in some colonial organisms and the notion of the unit-of-selection status (Rinkevich, 2000a). The modular idea is essentially a visual (morphological) and topological one (Rosen, 1986), and is hierarchically constructed on up to three levels of organization: primary modules or zooids; second-order modules, grouped zooids arranged in replicated patterns (may be called branches, such as branching corals or "systems", as in botryllid ascidians); and third-order modules, the daughter colonies or ramets (Ryland and Warner, 1986). With regard to body construction, the first- and the third-order modules (the zooid and the ramet) and the uppermost organizational level, the colony or genet, have captured most scientific interest.

Colonial structures emerge as iterative processes of successive layers of material (Kaandrop and de Kluijver, 1992). In branching colonial organisms, morphology is established through iteration of two structural units: modules of the first order (the zooids) and modules of the second order (the branches). Variations in the branching morphologies of colonial organisms are frequently correlated with a suite of life-history traits (Buss and Blackstone, 1991). A significant portion of relevant literature examines correlations between environmental qualities and morphometric analyses (either on the zooid, ramet, or genet level; Chamberlain and Graus, 1975; Bottjer, 1980; Sebens, 1984; Abelson et al., 1991; West et al., 1993; Helmuth et al., 1997; Johnson, 1997; Vago et al., 1998; and literature therein). While there is no doubt that environmental factors may tune phenotypic architecture, the common high fidelity of morphological structures reveals development homeostasis, probably controlled by the genetic background of the species of interest.

THE RATIONALE FOR COLONY ARCHITECTURE

Descriptions of colony growth can be supported by simple characterization of the rate at which new modules are generated, or can be based on the architecture and the 3-D

structures that emerge over time (Prusinkiewicz, 1998). Inherited traits in colony forms and the iterative processes that shape colonial structures may suggest that colonial architecture is the measurable outcome of developmental homeostasis pathways. Even the expression of high phenotypic plasticity, the outcome of the interactions between genotypes and heterogeneous environments (Callahan et al., 1997), may be rooted in the genetic background of the organisms and, as a result, can be evaluated by measurable codes and patterns. The study of colonial architecture, therefore, relies on the perception that colonial organisms are integrated wholes, rather than structural collections of modules (Rinkevich, 2000a), and compares changes in structures with an eye to a better understanding of heritable traits (Nijhout et al., 1986).

Different approaches to modeling colonial organization can be arranged along a polarized continuum. At one end is the idea that pattern formation of a colony is a morphologically rigid intrinsic process and genetically controlled. It is a centralized phenomenon working on the colony level. As a result, responses to environmental factors are achieved through the establishment of ecological races, genetically different ecotypes. At the other end of the continuum is the idea that colonial form is strictly flexible, shaped by trade-offs between different traits. Therefore, defining architecture is the science of defining a suite of characters that respond discretely to the environment. According to this notion, "variations" is the conserved character. Surprisingly enough, there are documented observations that even such phenotypic plasticity phenomena are probably also controlled by genetics, specifically by plasticity genes (Pigliucci, 1996; Callahan et al., 1997). One major pitfall of "trade-off" approaches is that many of them do not describe colony growth with explicit explanations for the processes that control colony allometry.

With regard to a branching system, the description of the organism in modular terms, the most commonly used illustration, is not too difficult. However, not recognizing interactions between colonial components may present some theoretical and practical difficulties (Bell, 1986). Since the implication of geometrical forms implies the use of mathematical tools, the rationale and assumptions based on the mathematical models employed are key issues in understanding the outcomes. For example, a variety of models used for development, including the formal one-dimensional algorithms (reviewed in Nijhout et al., 1986), did not address, and therefore missed, the possible relationship between gene expression and morphological features. The same problem applies to models developed by biologists that assume that morphologies are strictly determined by environmental features such as the availability of food particles (Abelson et al., 1993; West et al., 1993; Vago et al., 1998; and literature therein), although other studies (e.g., Amaral, 1994) clearly point out that changes in morphology cannot be explained solely by environmental variables.

More and more studies in the last two decades suggest an intrinsic order to branched growth, even in the most elaborate systems (Bell, 1986), although few have explicitly considered the problems and constraints posed by ontogeny on forms (Waller and Steingraeber, 1985). One such approach was to apply the "tree architectural models" to coral growth forms (Dauget, 1991a,b, 1994; and literature therein). The resulting

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comparisons revealed common rules for branching and ramifying axes systems, for the organization of these axes in identical architectural models, for the reiteration pattern in the course of growth, and also for the physiognomic variations correlated with environmental parameters. Other approaches have been to adapt mathematical models such as fractals and simulations of diffusion and flow (Waller and Steingraeber, 1985; Kaandorp and de Kluijver, 1992; Kaandorp and Sloot, 1997; Kaandorp, 1999; and literature therein) to branching patterns of colonial marine invertebrates. The above approaches were mainly employed by mathematicians.

Evolutionary biologists have employed other approaches. One of these is the adaptation of Waddington's (1942) theory regarding morphogenesis of colonial organisms (Buss and Blackstone, 1991). According to this approach, the development of a colony is represented as a problem in a dynamic system theory where colony reactions to environmental challenges are canalized; such adapted reactions result in one definite end point, regardless of minor variations in conditions during the course of development (Waddington, 1942; Buss and Blackstone, 1991). A second approach is to adapt the concept of heterochrony (the change in timing of development) to characterize colonial organisms as integrated wholes rather than as atomistic units (Blackstone and Yund, 1989; Blackstone and Buss, 1993). From this perspective, alterations of development during time-windows are analyzed as heterochronous changes intrinsic to the organism. However, since the study of heterochrony is based on comparable values (Blackstone and Yund, 1989), it is not equipped to reveal the biological and genetic bases for pattern formation. In addition, not all pattern-formations are age-based measurements. None of the above approaches, however, addresses the relationships between gene activities and morphological features (Nijhout et al., 1986).

BRANCHING—THE NATURE OF COMPLEXITY

Branching forms of sessile marine organisms (well represented by a variety of algae, sponges, cnidarians, and bryozoans) are examples of morphological systems constructed from many simple identical components, which together are capable of developing complex structures. Such modular forms may be constructed in the regular manner of a high degree of organization, or may be "bewilderingly complex and yet not haphazard" (Bell, 1986). Moreover, the existence of tissue connections between all modules in a branching colonial form most probably allows the transmission of cues, molecules, energy resources, and alarms between the zooids (Mackie, 1986). Characteristics such as the sharing of resources, communication, and coordination between remote parts of a branching structure (such as in the colonial hermatypic coral *Stylophora pistillata*) are therefore prerequisites for colonial holism and a fundamental attribute of "real" colonies, setting them apart from mere aggregates (Rinkevich, 2000a). Topics like growth patterns, senescence, and sexual vs. asexual reproduction (Jackson and Coates, 1986; Rinkevich and Loya, 1986; Rinkevich et al., 1992) are associated with colonial modularity. What has not been addressed in the relevant literature is the predicted genetic machinery, where highly specific and coordinated responses are evoked by arrays of

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regulatory genes acting at different hierarchical levels. One such example is the expression of homeobox genes (Miles and Miller, 1992; Cartwright et al., 1999).

A general colony form is schematically based on the lower-level units (the zooids) and reveals two aspects: (1) components of organization and (2) shape for every modular level presented. Branching organizations and branching shapes can occur at any modular level (Rosen, 1986). The higher-level unit, the whole branched entity, has generally been used as the primary unit for ecological interaction considerations. Since modules (the zooids and, in some cases, the branches or the ramets) are the building blocks for colony organization, these integrated, semi-autonomous subunits should also be considered. Analysis of regenerating isolated branches of the branching coral *Stylophora pistillata* has revealed that initial architectural complexities of the ramets may have a significant impact on the regeneration processes of the typical structure and complexity of an intact colony as a whole (Epstein et al., 2001).

No model has yet been developed for the study of branching modular organisms that permits analysis of phenotypic plasticity from both the architectural and genetic-trait points of view. Most data in the literature are fragmented and based on a variety of branching forms that reveal different aspects of trade-offs among multiple traits or across multiple developmental levels, and variable responses to different environmental challenges. I present here the branching scleractinian coral *Stylophora pistillata* as a model case study. Part of this approach has been described in a recent publication (Rinkevich, 2001). In brief, the approach is based on two working hypotheses: (1) that a *S. pistillata* colony represents the holistic structure, the functional unit of selection (*sensu* Tuomi and Vuorisalo, 1989; Rinkevich, 2000a) and (2) that coordination patterns are due to intrinsic, central colony-level control (*sensu* Harvell, 1991; Cartwright et al., 1999). In other words, genetics is a key factor in shaping the colony landscape.

STYLOPHORA PISTILLATA: TRANSITIONS IN TACTICS

Stylophora pistillata (Esper, 1797) is a widely distributed Indo-Pacific branching coral species characterized by rapid growth rate and a variety of color morphs, from dark-brown, purple, and yellow, to pale pink. In the Gulf of Elat (Red Sea) it is abundant in the lagoon, rear-reef, and reef flats, and common in the fore-reef (Loya, 1976), down to 60 m depth. Colonies of this species exhibit an axially rod-like growth form and each branch consists of numerous minute polyps (approximately 1 mm in diameter). *S. pistillata* is also an ecologically important key species, forming a substrate and habitat for many species of crabs (mainly Xanthidae and Alpheidae), fish (especially Pomacentridae and Gobiidae), as well as variety of cryptic organisms such as sponges, bivalves, polychaetes and others.

The astogeny of a typical *S. pistillata* colony is characterized by well-controlled developmental processes. Primary polyps start to deposit calcareous skeletons about 1 day following metamorphosis. One week thereafter, several additional polyps (usually six, similar to *Pocillopora*; Stephenson, 1931) are added extra-tentacularly from the peripheral tissue, to form a circle around the primary polyp. Growth rates of new polyps

over time are highly variable among young colonies (Frank et al., 1997). This kind of lateral expansion continues until, at some as yet unidentified stage, branches develop by apical growth. Only a single apical ramified structure is developed from each "lateral plate". New structures are then added, developing in conformity with the basic architectural rules of this species. These structures are reiterated complexes. An overview of a well-developed *S. pistillata* colony clearly reveals that the space between the up-growing and side-growing branches (see below) tends to be filled by the reiterated complexes (Dauget, 1991a,b), avoiding direct tissue-to-tissue contact of different branches.

The resulting symmetry of a typical *S. pistillata* colony approximates a sphere (Loya, 1976). Within the volume of the sphere, up-growing branches (UGBs) are primarily added by dichotomous fission at a branch-tip (Rinkevich and Loya, 1985a; Rinkevich 2000b, 2001). The apex of each axis (UGB) comprises several contiguous polyps. As a result of fast growth of one of the new formed branches (Rinkevich, 2000b), apical ramification usually forms unequally-sized axes. This is also reflected by the measured high (70%) variation in mean growth rates between all UGB tips of individual *S. pistillata* colonies. Tip growth ratios within newly formed dichotomous UGBs differ significantly from those of older branches, further emphasizing the within-colony genetic background for spatial configuration (Rinkevich, 2000b). In addition to the UGBs, many lateral, inward- and outward-facing branches (LBs) are formed. Outward-facing LBs elongate similarly to UGBs, adding further lateral volume to the colony's spherical structure (Loya, 1976). With regard to inward LBs, it could be predicted that after prolonged elongation they would encounter and fuse with UGBs. However, such fusing was never observed in intact *S. pistillata* colonies since these branches cease to grow at a certain point (Rinkevich and Loya, 1985a). The decrease in growth rates of inward LBs, the change in growth directionality of isogeneic branches that risk contiguity (Rinkevich and Loya, 1985a), the lack of fusion between branches of a colony, and the retreat growth occasionally recorded between closely growing branches of allogeneic colonies (Rinkevich and Loya, 1985b) reveal the existence of feedback mechanisms that "consider" current shapes and future growths within an architectural scheme of preplanned pattern formation. The possible appearance of chemical signals carrying biological activities that control these growth patterns has been suggested (Rinkevich and Loya, 1985a).

Following the expression of genetic components, internal transport of signals and nutrients may have strong impacts on pattern formation and allometry of many modular taxa, including *S. pistillata*. For example, translocation of photosynthates is recorded when *S. pistillata* colonies are allogeneically grafted with ^{14}C-labeled branches. The host colonies translocate the labeled photosynthates towards the regenerating portions (Rinkevich and Weissman, 1987), probably through the gastrovascular canals that connect different polyps. Some of the metabolites fixed daily are stored within the colony for future use in other parts or biological compartments. For example, planula-larvae, collected 1–7 months after the coral tissue was labeled with ^{14}C, contained significant amounts of labeled photosynthates (Rinkevich, 1989). Similarly, photosynthetically fixed products

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of a specific single day were still found to be contributing to newly formed tissues, months after labeling (Rinkevich, 1991). Reproductive activities are also developed and shaped at the colony level (Rinkevich and Loya, 1979), as are aging processes. In old, senescent colonies, reproductive activities and calcification rates decreased synchronically in all branches. New and old polyps exhibited senescence simultaneously, leading to complete tissue mortality (Rinkevich and Loya, 1986). Together, these findings reveal that *S. pistillata* (as, probably, in other branching colonial organisms) possess conserved "morphogenic codes" (Hogan, 1999), sets of species-specific rules that are expressed repeatedly and in harmony to develop the colonial landscape.

COLONIAL ARCHITECTURE: GENETICS VS. ENVIRONMENT

A fundamental requirement for understanding development is an appreciation of the relationships between genes and morphologies (Nijhout et al., 1986). Such relationships can be elucidated experimentally when the growth patterns of different-structured isolated branches (Fig. 1) or nubbins (isolated fragments the size of a single to a few polyps; Shafir et al., 2001; Fig. 2) from *S. pistillata* colonies are followed over time, and modification of the developed phenotypes are quantitatively and theoretically analyzed. The above characterizations are probably genetically controlled. However, they are also clearly affected by environmental and a variety of biological challenges. Colony architecture is probably a character shaped by selection, so trade-offs between that trait and other traits may define a suite of morphological responses, some influenced by genetics, others by epigenetic impacts. In *S. pistillata*, a developing colony responds to perturbations

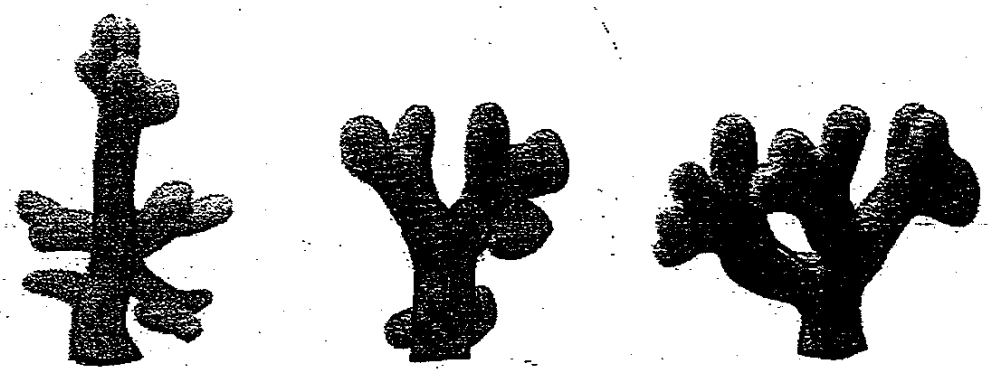

Fig. 1. Different pattern formation of colonial growth resulting from each initial fragment structure. Fragments a to c were taken from the same *S. pistillata* colony and represent the typical growth after 11 months of *in situ* culture. a = single tip branch that developed new lateral branches and relatively little apical growth; b = starting bifurcated branch that developed two ramified, well-defined sets of branches; c = ramified single branch that developed three well-defined sets of different branches. The initial sizes of the branches are confined within the black lines. Photographs taken by L. Shaish.

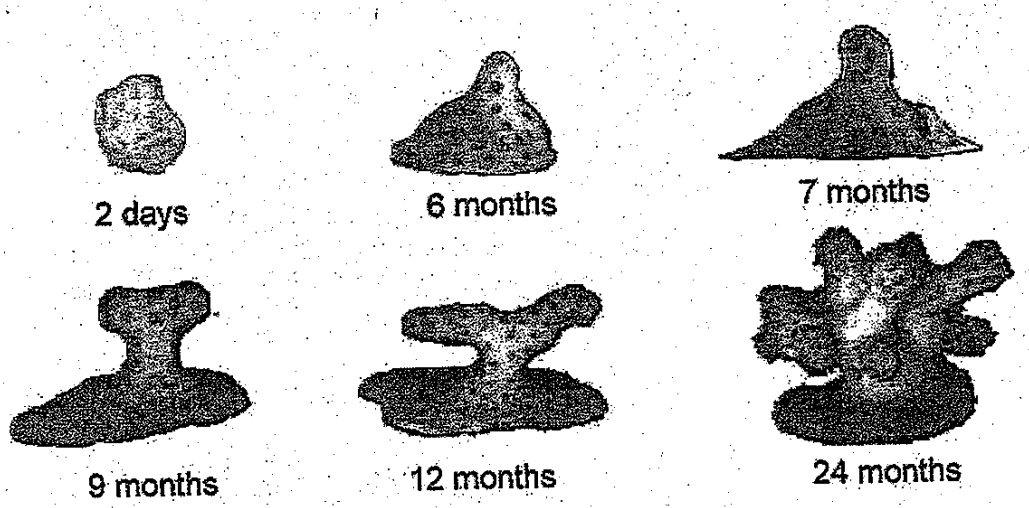

Fig. 2. From a nubbin, a structureless minute fragment of the branching coral *Stylophora*, to a whole, newly organized colony. Major steps in the well-organized establishment process of the species-specific architectural structure. These steps morphologically mimic the process involved in the astogeny of a *Stylophora* colony from settled and metamorphosed planula-larvae. Photographs taken by S. Shafir.

by a set of rules that "canalize" (Waddington, 1942) growth pattern to the typical species morphology. This was first illuminated by Loya (1976), who demonstrated that in broken *S. pistillata* colonies, the lost spherical structure is regained by a differential growth pattern involving fast growth in regenerating parts, together with a reduction in growth in the intact branches. Photosynthetic products are channeled to the regenerating parts (Rinkevich and Weissman, 1987).

Even a single separated polyp (or several separated polyps) from a *S. pistillata* colony has the capacity to develop a new colony (Shafir et al., 2001; Fig. 2). Therefore, as implied from the findings presented previously, an individual colony may be regarded as a "whole", where intrinsic orders of branch growths and related physiological parameters (such as sharing of resources between different branches, simultaneous aging processes, and reproductive activities; Rinkevich and Loya, 1979, 1983, 1984, 1985b, 1986, 1987; Rinkevich and Weissman, 1987; Rinkevich, 1991; Rinkevich et al., 1991) "produce" the structure we are familiar with. It is suggested here that the genetic blueprint of a colonial organism is activated to ensure that the new branches added and the enlargement of existing branches will acquire the rules for the species-specific landscape. Scientists could further explore the importance of genetics for colony landscape by creating simulating programs that are able to orchestrate the complex structure of a colony into mathematical language (Bell, 1986; Kaandorp and de Kluijver, 1992; Kaandorp and Sloot, 1997; Kaandorp, 1999) by application of architectural models to branching forms of colonies (Dauget, 1991a,b, 1994), by applying physical attributes to

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morphologies (Abelson et al., 1993), and by adopting other approaches for understanding morphologies (Blackstone and Yund, 1989; Buss and Blackstone, 1991; Blackstone and Buss, 1993; Cartwright et al., 1999).

A branching pattern develops by adding new components to an existing framework (Bell, 1986). In hermatypic branching forms, where past morphologies cannot be eliminated as the result of their calcium carbonate template, descriptions and analyses of dynamic branching processes along ontogenesis may reveal the rules of branching systems. Merely mimicking the rules for colony formation by assumptions that create simulated colonies is not enough, although in the past such approaches have provided insight into morphology. For example, Raup (1966) has shown that just four parameters were needed to simulate the gross form of a coiled shell and that actual specimens were not randomly distributed in the total spectrum of possible theoretical forms generated by computers. When simulating branch architecture, Bell (1986) distinguished between 3 different levels of biological reality: "blind", which is a simulated form oblivious to its environment; "sighted", where each step in the development is influenced by the environment but is unaware of its connectivity within the organism; and "self-regulatory", in which astogeny is controlled from within the organism using internal and possible external information. The "blind" aspect of branching architectures, in other words the genetic information, is the crucial level for construction. Some rigid forms may not accept the "sighted" or the "self-regulatory" aspects.

More than two decades of studies on different life history traits of *S. pistillata* have resulted in the accumulation of a vast amount of information regarding a variety of aspects that can be helpful when analyzing colony architecture. Flexibility and variations in colony landscape formation may be controlled by specific genetic rules, as may the general spherical structure of the colony and the iterative processes of branching. Although there is yet no direct evidence for this, the possibility of phenotypic plasticity in a colonial organism, being a construct of genetic rules for morphologies (Zilberberg and Edmunds, 1999), should be seriously taken into consideration when studying landscapes of marine invertebrate branching forms. Such an approach may also enforce controversial views regarding the "origin" of colony landscape. Evolutionary biologists may foresee the characteristic "species-species" phenotype as the outcome of selection processes favoring phenotypic plasticity or environmental specialization (canalization), leading to a phenotype consistently conveying the highest fitness (Weinig, 2000). On the other hand, developmental biologists may favor the phenotypic expression as an adaptive character where both genetics and environment shape the organism's landscape. These ideas should be taken into account when dealing with colony formation and landscapes of branching colonial organisms.

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