Chapter 1

Coupling sexual reproduction and complex multicellularity

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Understanding why multicellular organisms reproduce predominantly by sexual means has remained a major problem in evolutionary theory. A related question is the evolutionary origin of germ cell dimorphism and persistence of oogamy in all higher organisms. I propose, that by using the concept of facultative (optional) sexuality and the simple dualism of cellular reproduction versus functional cell differentiation it becomes possible to combine multicellularity, sexual reproduction, and oogamy in a novel way: a network model in which developmental and evolutionary information merge is presented. The model provides a logical framework for formal integration of theory and experimental data regarding evolutionary and developemntal biology of sexually reproducing multicellular organisms.

1.1 Introduction

The coupling of sexual reproduction and multicellularity is a key issue in evolutionary theory: natural selection should favor asexual reproduction as a more efficient way of producing offspring, yet sexual reproduction predominates in all major multicellular taxa [1, 2]. As a result, theories have been developed about mechanisms that would favor sexual as opposed to asexual reproduction, but testing these theories is difficult and the maintenance of sexuality in higher organisms has remained a mystery [3, 4].

It is a general notion that evolutionary success of multicellularity and success of sexual reproduction are coupled phenomena, but the evolutionary origin of multicellularity has received relatively little attention. Only few have addressed what the nature of the coupling might be [5, 6, 7].

In this study I address the coupling of sex and multicellularity as a dynamical system and expect that this compound system exhibits also novel behavior which is not attributable to its constituent subsystems *per se*. Furthermore I was motivated to find a model that can accommodate both facultative (optional) and obligate sexuality and to consider *obligate* sexuality a phenomenon related to multicellularity [8]. The model should conceptually couple sexual reproduction and multicellular development so that obligate sexuality may emerge from it as a special case.

1.2 A systems approach

Although I mainly considered the metazoa, I was particularly inspired by the green alga *Volvox carteri*. This model organisms alternates between asexual and sexual as well as multicellular and unicellular life cycle phases [9]. Could these life cycle transitions suggest a structure for analogous evolutionary transition? After a thorough theoretical analysis of published evolutionary and developmental literature I now propose a model that captures the interphase where where multicellular development meets the reproductive machinery. First the basic concepts are defined (summarized in Fig. 1.1) and then they are combind to produce a dynamical network model that is suggested to provide a general basis for evolution of sexual multicellular organisms and different kinds of life cycles.

Let us first consider the relationship between unicellularity and multicellularity. *Unicellularity* describes organisms where cells exist as individuals. They differentiate, grow, and divide (reproduce) independent of each other; cell cycle equals life cycle. This is the most common mode of reproduction in unicellular organisms.

The term *multicellularity* refers in this study to organisms that have more than one cell type and in which cells show co-ordinated behaviour [7].The so-called germ-soma division of labor results in two cell types. It forms when some cell of a multicellular entity retain reproductive potential while other cells differentiate to support the reproductive cells. This is observed for example in simple model organisms such as the cellular slime mold *Dictyostelium discoides* [10] and the green alga *Volvox* [9]

Sexual reproduction generally referst to a process that consists of the following: formation of sex cells (gametes) that can fuse, subsequent nuclear fusion which doubles the chromosome number, and finally meiosis which halves the chromosome number. A novel aspect of this work is that I have chosen *isogamy*, sexual reproduction through union of morphologically identical gametes, to be

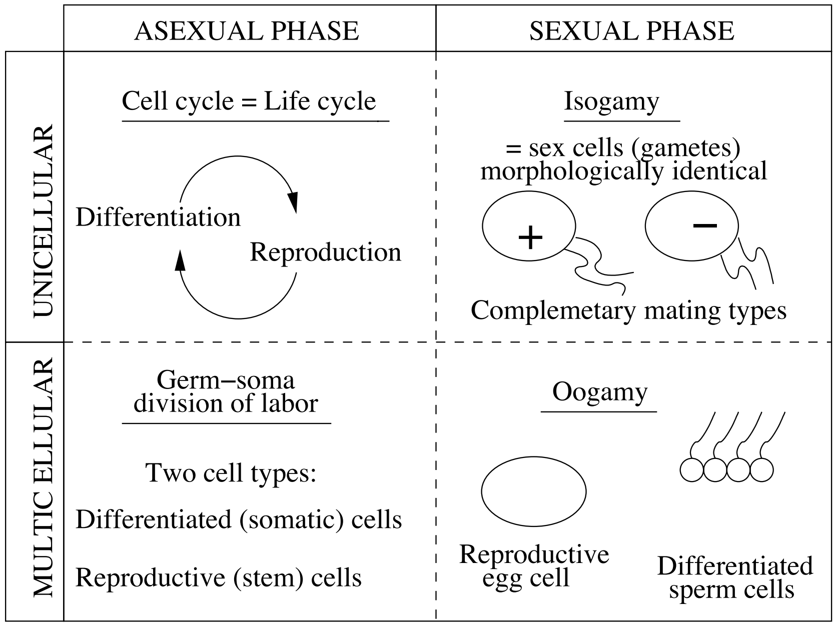

Figure 1.1: A two-by-two table with the following general biological attributes: asexual, sexual, unicellular, and multicellular. Asexual unicellularity (upper left quadrant) describes a situation where the cell cycle corresponds to the life cycle of the organism. Any given cell may exist and multiply independently. Simplest example for asexual multicellularity (lower left quadrant) is a case where some cells do not reproduce but support those that can. The example for sexual unicellularity (upper right quadrant) is the case where all sex cells (gametes) are morphologically identical, a condition known as *isogamy*. The phenomenon that I argue to sucessfully capture sexual multicellularity is oogamy (lower right quadrant) where the complementary gametes are different in terms of their developmental status.

the example that fulfills the conditions *unicellular & sexual* (Fig. 1.1, upper right quadrant). Many unicellular organisms are capable of occational sex and isogamy is commonly observed. But the sexual gametes of all higher organisms show sexual dichotomy.

Oogamy,which means reproduction through union of sperm and egg, is generally considered to be a pronounced form of anisogamy [11], but I argue here that this phenomenon is better understood in terms of the developmental processes that give rise to sperm versus eggs. Whereas an egg is itself a potential stem cell [12], the sperm cells *derive from* spermatogonial stem cells in a manner comparable to somatic (terminal) cell type differentiation. Although the genome of a sperm cell may be assigned potential immortality, the cell itself is terminally differentiated. Thus I argue that oogamy, generation of male versus female gametes, is the phenomenon where sexual reproduction and multicellular development merge (Fig. 1.1, lower right quadrant). To my knowledge, the evolution of gamete dimorphism has not been previously addressed from the point of view of developmental multicellularity.

1.2.1 State transition model

I have developed a dynamical state transition model where the basic aspects presented in Fig. 1.1 are combined to form a finite state machine structure.Fig. 1.2 displays a schematic graphical presentation of this model. In order to generalize the model, a state for *dormancy* has been added. Formation of dormant spores or zygotes is an important part of many complex life cycles.

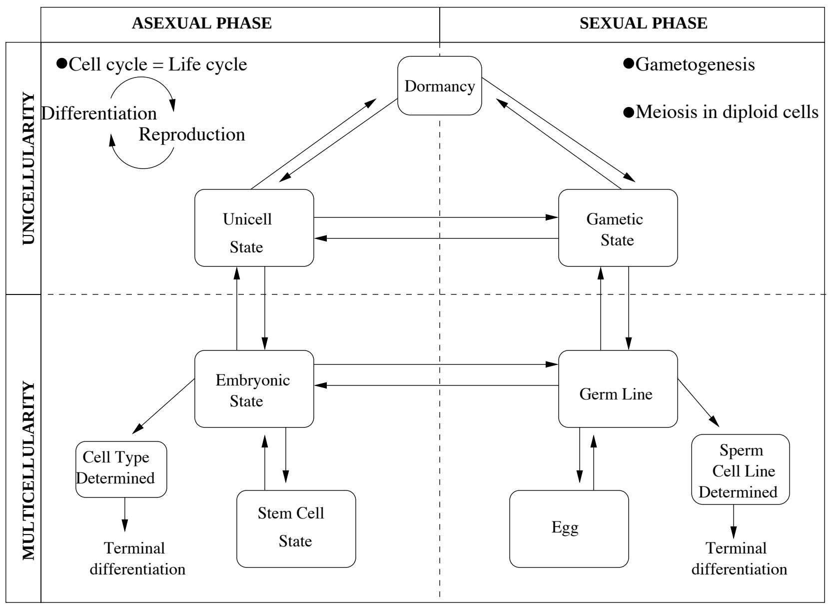

Figure 1.2: A schematic state transition model that combines multicellularity and sexual reproduction.The purpose is to show general structure and those key transitions that help to communicate the general idea. While some organisms, such as the *Volvox* exploit whole area of the graph, others only occupy some parts of it. In general: developemntally complex organisms tend to have simple lifecycles and simple organisms may have very complex life cycles.

I speculate that the model structure, as a whole, provides a basis from which embryonic multicellular development may emerge. Vegetative reproduction (somatic embryogenesis) involves what I have shosen to call the embryonic state, whereas the ability to alternate between asexual and sexual phase is assumed to derive from the unicellular ancestor. This ability is suggested to be the basis for the separation between sexual germ line and the rest of the body (soma). If some cells remain or are able to re-enter one of the four core states that can be used to move from one phase (quadrant) to another , the remaining cells of a multicellular entity may evolve freely and experiment with terminal differentiation. If cells of the asexual phase no longer are able to return to the states that allow reproduction, the reproductive function would be completely allocated to the sexual process which conceptually resides outside asexual embryonic development. This scenario could lead to rapid emergence of complex, sexually reprpoducing organisms.

1.3 Some implications

This model structure proposed in this paper is robust yet mallable and it can provide a formal framework for a combined analysis of evolution and development. My point of view is that of systems science. If the transition to developmental multicellularity establishes a dynamical system with novel overall structure, this creates a new level of organization which is not present in the world of unicells. This may be of relevance when one considers why plants and animals have are predominantly sexual and why these taxa diversified rapidly once they emerged.

Because the model can be viewed as a finite state machine, different routes through the states of the model produce strings of states, sequences, that vary in length and in the order of the states. Thus I argue, that the various types of life cycles of real organisms can be generated from this model and that the model can be used to study life cycle evolution in general.

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