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Essay

Evolution and development of budding by stem cells: Ascidian coloniality as a case study

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ABSTRACT

The evolution of budding in metazoans is not well understood on a mechanistic level, but is an important developmental process. We examine the evolution of coloniality in ascidians, contrasting the life histories of solitary and colonial forms with a focus on the cellular and developmental basis of the evolution of budding. Tunicates are an excellent group to study colonial transitions, as all solitary larvae develop with determinant and invariant cleavage patterns, but colonial species show robust developmental flexibility during larval development. We propose that acquiring new stem cell lineages in the larvae may be a preadaptation necessary for the evolution of budding. Brooding in colonial ascidians allows increased egg size, which in turn allows greater flexibility in the specification of cells and cell numbers in late embryonic and pre-metamorphic larval stages. We review hypotheses for changes in stem cell lineages in colonial species, describe what the current data suggest about the evolution of budding, and discuss where we believe further studies will be most fruitful.

Introduction

Studies of life histories are often theoretical descriptions of the selective forces that govern evolutionary transitions. Many studies have measured fitness tradeoffs between alternative forms or modeled the selective pressures that promote or prohibit a given type of life history modification, but few have attempted to reconstruct the developmental mechanisms that allow the evolution of these alternative adult forms (Buss, 1983; Felix and Barriere, 2005; Grosberg and Strathmann, 2007; Michod, 1999; Okasha, 2005; Ransick et al., 1996; Rutherford et al., 2007; Yajima, 2007). Most of the existing data on developmental change associated with life history evolution comes from comparative work on indirect and direct development in sea urchins and ascidians. In these taxa the developmental modifications and heterochrony that result in direct development, i.e., loss of the pluteus larva in urchins or loss of the tail of the tadpole larva in solitary ascidians, have been documented and studied in molecular and cellular detail (Jeffery and Swalla, 1992; Sly et al., 2003; Swalla and Jeffery, 1996).

Developmental biology need not be confined only to studying the molecular and cellular interactions that occur during the lifetime of an organism. Understanding the general importance of developmental modification(s) in evolution requires comparative study of closely related taxa with different modes of development. Here we describe this comparative evolutionary approach in the context of life history evolution in ascidians, by comparing the embryonic and germ cell lineages between solitary and colonial ascidians and envisioning how changes in fates or commitment of cells may facilitate the evolution of coloniality. These ontogenetic changes can either facilitate or restrain certain adult phenotypes, behaviors, or modes of reproduction providing an additional source of variation, often disregarded, at the population or species level that then undergo evolutionary processes of selection.

To understand the limits that development places on phenotypic evolution we first describe the mechanisms that cause cells to become co-opted into different functions during development. This process has constraints because cell lineages are determined in spatial position, timing, number, and by interaction with other cells (Azevedo et al., 2005). Changes in cell lineages and cell fates during development can be cell-autonomous (within the cell) or non-autonomous (outside the cell). Autonomous modifications include differential partitioning of cytoplasmic determinants during cell division and regulatory modifications of gene expression in particular cells, e.g., P-lineage specification by asymmetric cell divisions in *C. elegans* zygotes (Gönczy and Rose, 2005). Non-autonomous modifications include general or lineage specific changes that can

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affect rates of cell division or the timing of cellular fate determination, e.g., induction of neural and surface eye epithelia by Pax-6 via Fibroblast Growth Factor (FGF) and Bone Morphogenetic Protein (BMP) signaling in vertebrates (Donner et al., 2006). Autonomous and non-autonomous mechanisms can result in changes in the fate determination of existing cell lineages during development, or in the differentiation of novel cell lineages from multipotent stem cells.

Constraints on the scope of developmental modifications may bias the course of phenotypic evolution, or result in contingencies where one evolutionary novelty sets the stage for another in a stepwise manner. We propose that increases in egg and larval size associated with brooding opened previously inaccessible pathways to coloniality in ascidians by changes in the timing of specification of embryonic and adult stem cell lineages, facilitating the evolution of a new life history. The details of these developmental modifications may allow insights into how and why coloniality evolved in tunicates. Box 1.

Evolution of colonial life histories in tunicates

Evolutionary transitions from solitary to colonial tunicates (Fig. 1) are accompanied by multiple morphological, developmental, and reproductive changes, such as miniaturization of individual body size, brooding, and primarily asexual reproduction by budding (Davidson et al., 2004; Zeng et al., 2006). Phylogenies based on both morphological and molecular data suggest that the Tunicates are monophyletic (Fig. 2). The Tunicata includes Appendicularia, Stolidobranchia ascidians (Fig. 1E and F), Phlebobranchia ascidians (Fig. 1A and B), Aplousobranchia ascidians (Fig. 1C and D), and Thaliacea (Stach and Turbeville, 2002; Swalla et al., 2000; Tsagkogeorga et al., 2009; Turon and Lopez-Legentil, 2004; Zeng et al., 2006). The earliest tunicate fossil records date back the Cambrian or earlier (Fedonkin et al., 2012), however limited fossil evidence and unresolved clades in the phylogeny of tunicates makes it difficult to infer the directionality of life history transitions in many groups of colonial ascidians, but there

Box 1–Glossary of tunicate budding and stem cell terminology

Aggregate stolonial budding: Highly modified budding in pelagic tunicates (Thaliacea: Salpidae) of a side chain structure called a stolon. Each stolon consists of undifferentiated tissue on its proximal end, and a chain of aggregates of buds that become more differentiated towards its distal end (Fig. 2H) (Toselli and Harbison, 1977).

Brooding: Act of incubating the zygote either in specialized organs/tissues or simply within cavities of the organism; ascidian species may be either viviparous or ovoviviparous.

Commitment: Aspect of the intrinsic cell or tissue region which causes it to follow a particular pathway of development or fate (Slack, 1991).

Determination: Irreversible commitment of a cell or tissue region. Heritable after cell division (Slack, 1991).

Embryonic stem cell (ESC): Pluripotent stem cell lineage derived from early cleavage embryos. They are not likely present in solitary ascidians, but may be present in colonial species.

Peribranchial budding: Budding in colonial stolidobranch ascidians (e.g., *Botryllus, Botrylloides*) derived from an evagination of the outer epithelia surrounding the branchial sac and integration of mesendoderm and blood cells surrounding the branchial basket. Also referred as palleal or lateral budding (Fig. 1E,F and 2A).

Pyloric budding: Budding in colonial aplousobranch ascidians (e.g., *Didemnum, Diplosoma*) derived from two opposite and simultaneously developing buds in the epicardial region at the base of the endostyle or oesophagus of an individual. One bud will differentiate into a new branchial sac and fuse to the old abdomen, and the other differentiates to a new abdomen that fuses the old branchial sac, thus forming two new individuals (Fig. 1D and 2G).

Progenitor cell: Generic term for any dividing cell with the capacity to differentiate. Includes putative stem cells in which self-renewal has not yet been demonstrated (Smith, 2006).

Progenitor stem cell: Any dividing cell with the capacity to self renew and differentiate.

Precursor cell: Generic term for cells without self-renewal ability that contribute to tissue formation (Smith, 2006).

Potency: The range of commitment options available to a cell (Smith, 2006). 'Restriction of potency' can be acquired by either cell lineage commitment or determination.

Pluripotent: Able to form all cell lineages of the body, including germ cells. Ex. *Perophora* adult lymphocyte-like blood cell (Freeman, 1964), or ESCs in mammals (Smith, 2006).

Multipotent: Can form multiple lineages that constitute an entire tissue or tissues. Ex. Hematopoietic stem cells (Smith, 2006).

Unipotent: Forms a single lineage. Ex. Germline stem cells.

Reprogramming: Increase in potency. Occurs naturally in regenerative organisms (dedifferentiation) (Smith, 2006).

Stem cell: A cell that has the ability to undergo an asymmetric division giving rise to one cell for self-renewal identical in fate to its precursor, and another one with a more restricted fate. The presence or acquisition of these features in a cell is generally referred to as **stem-cellness**.

Stolon: Vasculature that connects individuals of colonial ascidians that are generally separated in their own tunic. In contrast to the vasculature of botryllid colonies, the stolon contains in its lumen a single layered epithelium, i.e., the septum that allows a two-directional blood flow.

Stolonial budding: Budding in colonial aplousobranch and phlebobranch ascidians (e.g., *Perophora*) that occur at regular intervals of the stolon, the septum is involved in the budding process (Fig. 1B and 2D).

Strobilation: Budding in colonial aplousobranch ascidians (e.g., *Aplidium*) that occur from constriction of pieces that detach at the posterior-abdominal end of individuals (Fig. 1C).

Of abdomen (Type I): Results from epidermal constrictions that form buds which contain gut tissues and epicardium, an abdominally located epithelium (Fig. 2E).

Of abdomen and postabdomen (Type II): Results from epidermal constrictions that form buds which always contain epicardium, but gut tissues only in the branchial-most buds (Fig. 2F).

Terminal budding: Budding in colonial phlebobranch ascidians (e.g., *Perophora*) that occurs at the tip of the stolon by the release of a pelagic bud composed of epidermis and mesendodermal tissue, such as the septum (Fig. 1C).

Vascular budding: Budding in colonial stolidobranch ascidians (e.g., *Botryllus, Botrylloides, Symplegma*) that occur as an encapsulation of blood derived cells by vascular epithelia at sporadic sites of vessels connecting the zooids embedded in a common tunic (Fig. 1E and 2B).

Zooid: An individual of an ascidian colony.