

Hatching enzyme of *Volvox*: a possible implication in the evolution of multicellularity

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Volvox as a model organism

A green alga *Volvox carteri* is an attractive model organism for studying the evolution of multicellularity because of its simple body plan consisting of only two cell types. A typical young spheroid of *V. carteri* consists of about 16 reproductive cells called gonidia and approximately 2000 biflagellate somatic cells that are morphologically similar to unicellular green alga *Chlamydomonas reinhardtii*. Since the divergence time of *V. carteri* and *C. reinhardtii* estimated by molecular phylogenetic analysis was as recently as 50-75 million years ago (Rausch et al. 1989), it is considered that relatively simple alterations in the genetic system of the unicellular ancestor gave rise to multicellular organisms (Kirk 2005). Development of tools for molecular genetic study in *V. carteri*, such as genetic transformation by microprojectile bombardment and gene cloning by transposon-tagging, enabled researchers to use this organism as a model for studying the genetic and cytological control of morphogenesis (Kirk 2005; Kirk and Nishii 2001; Miller 2002).

Extracellular matrix and hatching protease

V. carteri belongs to the order Volvocales that include a group of closely related organisms that range in complexity from unicellular organisms (e.g. *C. reinhardtii*), through colonial organisms with various cell numbers (e.g. *Gonium* and *Pandorina*), to multicellular organisms (e.g. *V. carteri*) (Kirk 2005). Individual cells of many of these algae are held together in the body of adult organisms by extracellular matrix (ECM), the major components of which are glycoproteins (Hallmann 2006). The cells of unicellular species are also surrounded by ECM, that is usually called 'cell wall', that is homologous to the ECM of the colonial and multicellular relatives. In the life cycle of volvocine algae, daughter organisms hatch out of parental bodies degrading the parental ECM after

the daughter organisms have matured (Fig. 1). In *C. reinhardtii*, hatching of daughter cells from their mother cell walls occurs within several hours after cell division. In contrast, in *V. carteri*, hatching of juveniles occurs after more than a day after the first cell division of the reproductive cells. Various developmental events including cleavage divisions to increase cell number take place before hatching. Also, in colonial relatives of *Volvox*, cell cleavages to increase cell numbers occur before hatching in individual organisms. Thus, heterochronic delay in the timing of hatching that allows embryos to increase cell

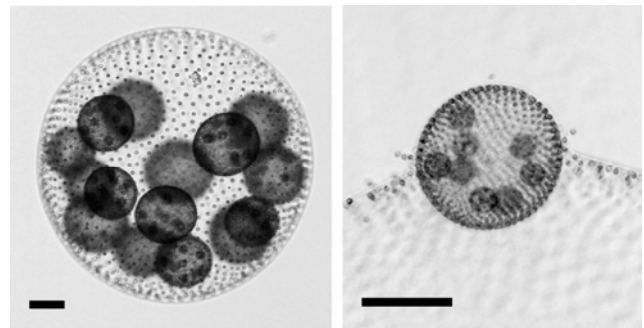


Figure 1: Mature spheroid of *Volvox carteri* (left) and a daughter spheroid in the process of hatching (right). Bars = 0.1 mm.

number is one prerequisite for the evolution of multicellularity in volvocine algae. Concerning the hatching process in *Volvox carteri*, it had been known that an enzymatic activity that degrades parental ECM is detected in the culture medium during and after hatching. Recently, molecular details of the enzyme were revealed (Fukada et al. 2006). This hatching enzyme is a serine protease that accumulates in the embryos as a precursor containing N-terminal transmembrane domain. The accumulated enzyme is secreted exactly at the timing of hatching after removal of the N-terminal domain, suggesting that post-translational regulation is involved in the strict control of the timing of hatching. Also suggested in the study is that the substrate of the protease is synthesized and integrated into the ECM only after spheroids are liberated from parental spheroids, since ECM of young spheroids just after hatching is resistant to the enzyme whereas ECM of the spheroids in later stages become susceptible. Thus, hatching of *V. carteri* is regulated at two levels: one is at the level of the activation and secretion of the hatching enzyme and the other is at the level of the synthesis of the substrate and its integration into ECM.

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It is known that, in mammals, degradation of ECM by proteases secreted from cancer cells are involved in invasion and metastasis of cancer. Although these events are not welcome for higher organisms, the combination of ECM connecting cells and proteases degrading ECM may have played an important role in the evolution of multicellularity in volvocine algae and possibly in the early life on earth.

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