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REVIEWS

Comparative Analysis of Embryonic Inversion in Algae of the Genus *Volvox* (Volvocales, Chlorophyta)[1]

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Abstract—Recent literary data on inversion (turning inside out) in the embryos of flagellated algae of the genus *Volvox* are critically analyzed. In this process, active changes in the shape of embryonic cells and the displacement of intercellular cytoplasmic bridges play an important role. After inversion, the flagella appear on the outer side of the young colony and provide its motility. Within the genus *Volvox*, two main modes of embryo inversion have been recently established during the asexual developmental cycle—inversion of type A and inversion of type B—represented by the two species most thoroughly studied, respectively, *Volvox carteri* f. *nagariensis* and *V. globator*. However, the published opinion that the inversion of *V. aureus* embryos is of the type B seems to be doubtful. Comparative and evolutionary aspects of embryonic inversion in *Volvox* are discussed with the use of data on other genera of colonial volvocine algae.

Keywords: algae, embryonic inversion, evolution, morphogenesis, *Volvox*

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The green flagellated alga *Volvox*, consisting of two types of cells, somatic and reproductive, is a valuable model organism of contemporary developmental biology (Kirk and Nishii, 2001; Matt and Umen, 2016; Desnitskiy, 2017). The asexual reproductive cycles of *Volvox* and several other related members of the family Volvocaceae (e.g., *Pleodorina, Eudorina, Pandorina*) include growth and a series of consecutive divisions of gonidia (asexual reproductive cells), embryonic inversion, growth of young organisms, their release from the parent, etc. The crucial step of *Volvox* morphogenesis is the process of inversion of the embryos (young developing colonies) that occurs shortly after the completion of cell division, when a hollow spherical mass of cells arises. At this stage of development, the inner and outer sides of the young colony are formed by the nuclear (future flagellate) and chloroplast ends of the cells, respectively. In the process of inversion, the hollow spheroid turns inside out through the phialopore—a small opening in the anterior pole. Thus, the flagella appear on the outer surface of a spherical colony and can subsequently provide its motility.

Inversion was described in several *Volvox* species during the first half of the 20th century (Powers, 1908; Janet, 1923; Zimmermann, 1925; Kuschakewitsch, 1931; Pocock, 1933a, 1933b). However, the details of this process at the cellular level were elucidated much later, as a result of research on the development of *Volvox carteri* f. *nagariensis* (Viamontes and Kirk, 1977; Kirk, 1998; Kirk and Nishii, 2001; etc.). Inversion begins within 30–60 min after the end of gonidial cleavage and takes approximately 45 min to complete. The first event is the change in the shape of all presumptive somatic cells of the embryo, which are connected by thin cytoplasmic bridges (the result of incomplete cytokinesis during cleavage), from pear-shaped to spindle-shaped. As a result, the volume of the embryo undergoes some decrease. Then the cells around the phialopore become bottle-shaped with long thin processes that look outward. Simultaneously, these cells are displaced in such a way that the cytoplasmic bridges now connect not the middle parts of the cells as before but the tips of their processes. As a result, a mechanical stress seems to arise, which is resolved by means of turning the phialopore lips outward (Fig. 1). Further, the inversion continues, since the change in cell shape into a bottle-like one and simultaneous displacement of these cells relative to the bridges occur in an area that is more distal to the phialopore. After passing through the region of the greatest curvature, the cells become transformed from bottle-shaped to cylinder-shaped. By the time when the wave of changes in the cell shapes reaches the opposite pole, the entire young colony is turned inside out, and the flagella appear on its outer side.

Mutants of *Volvox* that do not undergo colony inversion after the completion of cell division series are known (Kirk, 1998; Ueki and Nishii, 2009). There-

[1] The article was translated by the author.

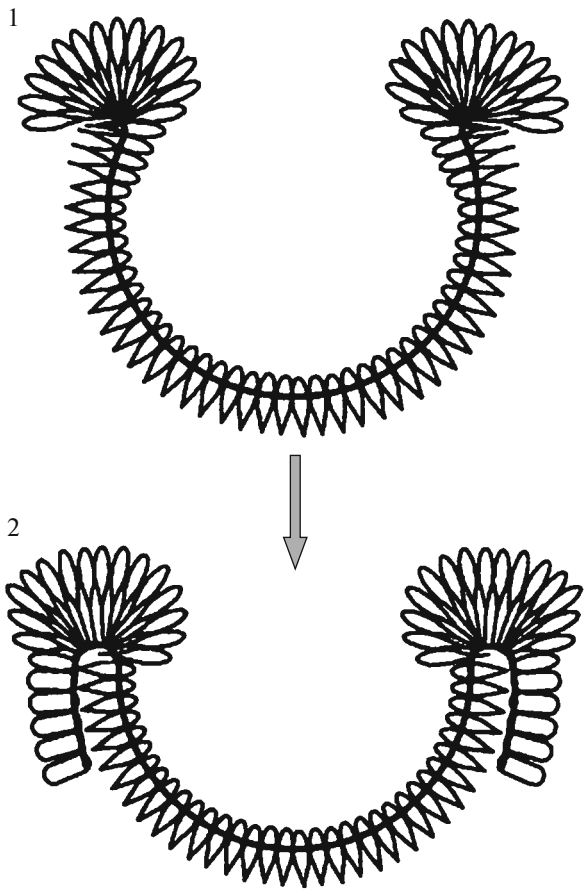

Fig. 1. Two consecutive stages of embryo inversion in *Volvox carteri* f. *nagariensis* (simplified from Kirk and Nishii, 2001). 1—"early" inversion; 2—"medium" inversion.

fore, a study of the *InvA* gene encoding the kinesin protein essential for inversion is of particular interest (Nishii et al., 2003). The protein is synthesized in the course of embryogenesis (cleavage and inversion), resides in intercellular cytoplasmic bridges, and provides a driving force for the colony inversion of *V. carteri* f. *nagariensis*. The *InvA*$^-$ mutant exhibits only the earliest steps of inversion: the elongation of cells (the acquisition of a spindle-like shape) and the initial opening of the phialopore lips, but there is no displacement of the cells relative to cytoplasmic bridges, and further inversion is completely blocked. This work well complements the previous study of the same group (Nishii and Ogihara, 1999), in which it was shown that actomyosin plays an important role in the propagation of the area of the cell sheet flexion from the anterior to posterior hemisphere of *Volvox* embryo at later steps of inversion. On the other hand, the processes of displacement and changing the shape of individual cells do not depend on actomyosin. Note that Nishii et al. (2003) discovered the *iar* gene (an ortholog of the *InvA* gene) in the genome of unicellular alga *Chlamydomonas reinhardtii*, which also encodes kinesine, similar in amino acid sequence to kinesin of *V. carteri* f. *nagariensis*. The function of this protein in the inversionless *Chlamydomonas* is still unclear (Umen and Olson, 2012; Matt and Umen, 2016).

Experimental-morphological studies performed on *V. aureus* (Kelland, 1977) and *V. tertius* (Ireland and Hawkins, 1981) were in good agreement with the data on the model species *V. carteri* f. *nagariensis* (Viamontes and Kirk, 1977), but they showed that some variations might be in details of inversion among different *Volvox* species. Nonetheless, Hoops et al. (2006) assumed that the basic mechanisms of inversion (changes in the shape of embryonic cells and the active role of intercellular cytoplasmic bridges) are similar not only in different species of *Volvox* but even in species from different genera of the family Volvocaceae.

However, very important data have been recently obtained during the analysis of asexual development of *V. globator* (Hallmann, 2006; Höhn and Hallmann, 2011), which showed that the inversion processes in different species of the genus *Volvox* are more diverse than previously thought. In particular, shortly after the end of cleavage in *V. globator* embryo, there is a slight decrease in the volume of its posterior hemisphere and it turns out. Only after that the phialopore opens at the anterior pole and the anterior hemisphere turns out, followed by the closure of the phialopore (Fig. 2). Thus, two main modes of inversion of *Volvox* embryos were established: the inversion of "type A" and the inversion of "type B," represented by the two species most thoroughly studied, respectively *V. carteri* f. *nagariensis* and *V. globator* (Hallmann, 2006; Höhn and Hallmann, 2011). The principal difference between these two types of inversion is that this process begins at the anterior pole of the embryo in the first case, while in its posterior hemisphere in the second case. Coordinated displacements of cells relative to the system of intercellular cytoplasmic bridges play, along with changes of the cell shape, an important role in the inversion process in embryos of both *Volvox* species. In *V. globator*, though, the spindle-shaped cells could be observed not in the entire embryo but only in the posterior hemisphere at the stage of its compression. The consideration of mathematical models of the process of *Volvox* embryo inversion (with a focus on the data on the morphogenesis of *V. globator*), which have been published recently (Haas and Goldstein, 2015; Höhn et al., 2015), is not within the scope of this paper.

We should briefly discuss data on other representatives of the genus *Volvox*, in which, however, the features of embryo inversion have been studied to a lesser extent than in *V. carteri* f. *nagariensis* and *V. globator*. The literature contains relevant information on the morphogenesis in *V. africanus* (Pocock, 1933a), *V. aureus* (Darden, 1966; Kelland, 1977), *V. capensis* (Pocock, 1933b), *V. gigas* (Pocock, 1933a), *V. rousseletii* (Pocock, 1933b; McCracken and Starr, 1970) and

V. tertius (Pickett-Heaps, 1970; Ireland and Hawkins, 1981; Hallmann, 2006). In the abovementioned articles on *V. globator* (Hallmann, 2006; Höhn and Hallmann, 2011), it was stated that *V. africanus, V. gigas*, and *V. tertius* are characterized by an inversion of type A (similar to *V. carteri* f. *nagariensis*). This point of view seems to me quite reasonable. In addition, I would like to note that all four mentioned *Volvox* species with inversion of type A have large gonidia, cleaving without cellular growth, while the other mentioned *Volvox* species have small gonidia and embryonic cells grow during the intervals between consecutive divisions (Herron et al., 2010; Desnitskiy, 2016).

On the other hand, an opinion was expressed (Hallmann, 2006; Höhn and Hallmann, 2011) that the type B inversion (similar to *V. globator*) is characteristic of *V. aureus, V. capensis, V. dissipatrix*, and *V. rousseletii* (species with small gonidia). However, such a point of view seems to me valid only for *V. capensis* and *V. rousseletii*. In the literature, there are no data on the features of the embryo inversion process in *V. dissipatrix*, and inversion studies in *V. aureus* (Darden, 1966, p. 242, Figs. 10–15; Kelland, 1977, p. 377, Fig. 11) show that it differs significantly from type B inversion. Note that, according to Pocock (1933a, p. 485), "in *V. africanus*, inversion is of a similar type to that in *V. aureus*." As mentioned above, *V. africanus* has an inversion of type A. In the future, of course, it would be important to conduct a more detailed analysis of morphogenesis in the cosmopolitan alga *V. aureus*. At present, it is not possible to draw conclusions about the existence of a correlation of inversion type in *Volvox* with the size of mature gonidia and the presence or absence of cellular growth during the intervals between consecutive cleavage divisions.

Thus, within the genus *Volvox*, which includes 22 species distributed among four taxonomic sections (Nozaki et al., 2015), more or less detailed descriptions of the process of embryo inversion are available for eight species. Asexual colonies with inversion of type B (*V. capensis, V. globator, V. rousseletii*) are characteristic only of members of the taxonomic section *Euvolvox*. This section is distinctly detached in a phylogenetic respect (Herron and Nedelcu, 2015; Nozaki et al., 2015) from the three remaining sections, which include the other mentioned *Volvox* species.

Colonies of species with inversion of type B, as a rule, consist of more cells than colonies of species with inversion of type A (*V. africanus, V. carteri, V. gigas, V. tertius*). However, this pattern is not absolute and cell numbers can overlap in some species: for example, the asexual colonies of *V. carteri* and *V. rousseletii* consist, according to our data (Shelton et al., 2012), respectively, of 587–5024 and 3106–12971 cells. Nevertheless, data on sexual reproduction and development in *V. rousseletii* (Pocock, 1933b) show that a relatively small number of cells in the embryo can impose certain "developmental constraints" on the process of morphogenesis. The miniature embryo of this *Volvox* species formed as a result of zygote germination turns inside out when it consists of only 128, 256, or 512 cells. On the other hand, a sperm packet formed as a result of a series of divisions in androgonidium (male initial cell) also undergoes inversion when it reaches 256- or 512-celled stage. In both cases, the process of turning inside out proceeds differently from that during the asexual development of *V. rousseletii* and, in the light of the concept of two main types of inversion in *Volvox* (Hallmann, 2006) may be classified as an inversion of type A.

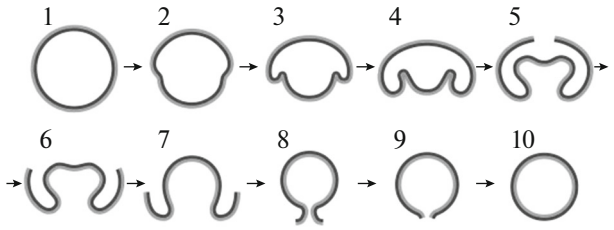

Fig. 2. Ten consecutive stages of the entire inversion process in *V. globator* (simplified from Höhn and Hallmann, 2011). Phialopore opens only at stage 5 on the anterior (upper) pole of the embryo and closes after stage 9 at the posterior (bottom) pole.

We will now proceed to a brief consideration of the data on the morphogenesis of some more primitively organized colonial volvocine algae. In the process of inversion of 8–16-celled *Pandorina morum* (Fulton, 1978; Hallmann, 2006) as well as 16–32-celled *Eudorina elegans* (Marchant, 1977), *Eudorina unicocca* (Hallmann, 2006) and *Platydorina caudata* (Iida et al., 2011), all cells of the embryo that completed cleavage simultaneously undergo a change of shape. Let us recall that the mature colonies of *Pandorina* and *Eudorina* are spherical, whereas the young colonies of *Platydorina* undergo the so-called process of "intercalation" shortly after the end of the inversion and become flat.

Pleodorina californica, the closest relative of *Volvox*, has spherical colonies consisting of 64 or 128 cells. During the inversion of *Pleodorina* (Höhn and Hallmann, 2016), the embryonic cells undergo a change in shape not simultaneously (unlike *Pandorina, Platydorina*, and *Eudorina*), but it proceeds in a wave-like manner towards the posterior pole, resembling the inversion of type A in *Volvox*. On the other hand, only the cells in the posterior hemisphere of the *Pleodorina* embryo acquire a spindle-like shape, similar to the type B inversion. Thus, various changes in the process of the *Pleodorina* embryo inversion might have led, in the course of evolution, to an inversion of type A or type B in algae of the genus *Volvox*. However, it is still difficult to say which of the two modes of inversion is more advanced in an evolutionary respect.

Finally, it should be noted that, among the green algae of the order Volvocales, exists the genus *Astrephomene*, in which the spherical colonies consist of 32 or 64 cells, but there is no inversion (Yamashita et al., 2016). In this case, embryonic divisions are oriented in such a way that the flagellate ends of cells look outward immediately after the completion of cleavage, and the young asexual colony of *Astrephomene gubernaculifera* does not need to turn inside out. In the cleaving embryo of this alga, there are intercellular cytoplasmic bridges (as in other colonial Volvocales). Therefore, it may be assumed that a homolog of the abovementioned invA (or similar motor protein) is localized in the bridges, which is important for proper orientation of cells during the cleavage process. Certainly, this hypothesis (Yamashita et al., 2016) about the peculiarities of "alternative evolution" in the genus *Astrephomene* requires experimental verification.

There was a traditional point of view (Ettl, 1983) that inversion does not occur during development of the 8–16-celled colonies of *Gonium pectorale*. However, according to recent data (Hallmann, 2006; Iida et al., 2013), a partial inversion proceeds in the course of ontogeny of this alga after the completion of a short series of three or four divisions; flagellate ends of cells temporarily appear on the concave side of embryo. But complete inversion does not occur, the degree of curvature gradually decreases, and the young colony acquires the final form of a flat or slightly convex plate (in the latter case, the flagellate ends of cells look outward).

In the literature of recent years, it has sometimes been attempted (for example, Keller and Shook, 2011) to compare the inversion of *Volvox* with gastrulation, the most important morphogenetic process during early development of multicellular animals, as a result of which the formation of germ layers occurs. Inversion of *Volvox* embryos was even called green algal "gastrulation" (Matt and Umen, 2016). The presence of cytoplasmic bridges, due to which neighboring cells of the embryo occupy a fixed position relative to each other, is certainly an important feature of the inversion process in *Volvox* compared to animal gastrulation. Note that, in some species of *Volvox*, the intercellular bridges are destroyed shortly after the end of the inversion, while they are retained in adult colonies in other species (Desnitskiy, 2014). Besides, gastrulation in Metazoa usually occurs along with sufficiently active proliferation of embryonic cells, whereas inversion in *Volvox* occurs after the end of the cellular division period.

Inversion of embryos occurs not only in the ontogeny of colonial volvocine algae but also in the early embryonic development of calcareous sponges (Calcarea), which constitute one of the classes of the type Porifera (Ivanov, 1971; Ereskovsky, 2010; Fortunato et al., 2012; Lanna and Klautau, 2012). However, details of inversion have been studied in the calcareous sponges not so thoroughly as in *Volvox*. Interestingly, there is a well-grounded opinion that the representatives of the type Porifera have neither germ layers nor gastrulation (Ereskovsky, 2010; Dondua and Kostyuchenko, 2013). The fact that the embryo inversion in the calcareous sponges is by no means a gastrulation provides, from our point of view, an additional support to the idea that the inversion of embryos in *Volvox* (lacking germ layers, of course) is also a process principally different from gastrulation.

In conclusion, let us note that turning the body inside out and changing the disposition of the germ layers occur during late stages of the ontogeny in *Polypodium hydriforme*, which is a parasitic cnidarian according to modern data (Okamura and Gruhl, 2016). However, this process in *Polypodium* is poorly studied (Raikova, 1994) and it is difficult to compare it with the inversion of *Volvox*.

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