



(Short communication)

On ecological aspects of the evolutionary reorganizations of *Volvox* ontogeny

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ABSTRACT

Our previous investigations have shown that the green freshwater algal genus *Volvox* is characterized by considerable diversity in the details of asexual reproduction with respect to the rate, diurnal rhythms and light/dark control of asexual reproductive cell divisions. These traits, being simultaneously developmental and ecological, correlate with the data on latitudinal distribution of *Volvox* species. In an attempt to understand how this diversity might have arisen during evolution, we use the published data on paleoclimatology and continental drift in the past as well as some information on the migrating waterfowl, which are today the vectors responsible for green freshwater algae transportation and dispersal.

Keywords : algal geography, Cenozoic, eco-evo-devo, reproductive cell division, zygotes, *Volvox*.

The genus *Volvox* (Volvocaceae, Chlorophyta) includes 22 species of spheroidal flagellated algae (Nozaki *et al.* 2015) and provides an opportunity to study the molecular-genetic mechanisms of development, differentiation and evolutionary transformations of ontogeny in a relatively simple system consisting of two types of cells, somatic and reproductive (Ferris *et al.* 2010, Nishii and Miller 2010, Nordhues *et al.* 2010, Prochnik *et al.* 2010, Hallmann 2011, Hanschen *et al.* 2014, Matt and Umen 2016, Grochau-Wright *et al.* 2017). However, this report is devoted to a topic that usually does not attract the attention of *Volvox* researchers: the analysis of some ecological aspects of the evolution of its development and reproduction.

In the laboratory cultures of several *Volvox* species (such as *Volvox carteri* and *V. spermatochaera*) as well as in more primitively organized colonial volvocine algae (such as *Pandorina morum*, *Eudorina elegans*, *Pleodorina californica*), a prolonged period of light-dependent growth of gonidia (asexual reproductive cells) is accompanied by a series of rapid divisions without cellular growth that can take place in the darkness (Desnitskiy 1984, 2008a, Herron *et al.* 2010). Our phylogenetic analysis shows that this type of development is ancestral within the family Volvocaceae, whereas the type of development with slow and light-dependent gonidial cleavage (for example, in *V. aureus*, *V. globator* and *V. tertius*) is derived and evolved in three evolutionary lines of the genus *Volvox* (Herron *et al.* 2010). In these species of *Volvox* with slow cleavage, the period of gonidial divisions is extended to at least two or three days. The divisions start in the morning of the first day, pause at night, recommence in the morning of the second day, stop at night again, etc. It has been found (Desnitskiy 2008b) that *V. aureus* is able to complete the asexual development cycle under the cultivation regime of 8 h light/16 h dark (instead of the standard for all *Volvox* species laboratory regime of 16 h light/8 h dark). The growth and development in cultures of *V.*

aureus proceed under conditions of short photoperiod, though at a low rate: the asexual cycle duration increases from 4-5 to 8-9 days (due to temporary interruptions of divisions during long dark periods). By contrast, in *V. carteri* cultures, the gonidial cleavage does not occur under such a light-dark regime (8 h light/16 h dark); the development stops and the cultures die within a few days exactly as if they were in complete darkness all this time. Thus, *V. carteri* cleavage either rapidly proceeds under sufficiently long photoperiod (at least 9-10 h) or does not start at all after a shorter photoperiod (Desnitskiy 1984).

It is appropriate to remark that according to our classification of asexual development patterns in the genus *Volvox* (Desnitskiy 2008a, 2016, 2017, Herron *et al.* 2010); species with rapid and light-independent gonidial divisions represent the first and second developmental programs, whereas species with slow and light-dependent gonidial divisions represent the third and fourth developmental programs. An example of ontogenetic diversity of *Volvox* is represented in Fig. 1.

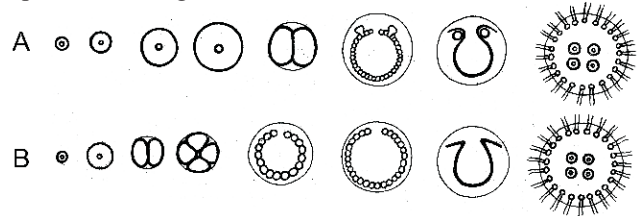


Fig. 1. Diagrammatic representation of crucial steps of asexual development (gonidial growth and cleavage followed by embryo turning inside out) in two species of *Volvox*. A. *V. carteri* is characterized by large and rapidly dividing gonidia as well as an early segregation of two cell lines: relatively large germinal and relatively small somatic initials (the result of asymmetric cleavage divisions). B. *V. aureus* is characterized by small and slowly dividing gonidia; there is no segregation of cell lines during gonidial cleavage. More detailed information about development in these and other species may be found elsewhere (Desnitskiy 2008a, 2016, 2017, Herron *et al.* 2010).

Data on the geographical distribution of all representatives of the genus *Volvox* were collected and identified cosmopolitan species (*V. aureus*), species recorded on several continents (e.g., *V. africanus*, *V. carteri*, *V. globator*, *V. tertius*), and species with local distribution (e.g., *V. gigas*, *V. powersii*, *V. spermatosphaera*) were identified (Desnitskiy 2008a, 2016). An attempt was made to trace a correlation between the latitudinal distributions of *Volvox* species and the type of light-dark control during cycles of asexual development. It turned out that in the relatively high latitudes of the Northern Hemisphere (northward of 52-57° N) only *V. aureus*, *V. globator* and *V. tertius* occur, in which slow gonidial divisions begin in the morning and the process of cleavage is temporarily blocked at night. It is possible that these features have an adaptive significance under the conditions of long summer days and they might have been important for the formation of the modern (Holocene) flora of colonial volvocine algae in the Northern Hemisphere. Interestingly, in the Southern Hemisphere southward of 35-36° S, only five species with slow and light-dependent gonidial cleavage occur: *V. aureus*, *V. barberi*, *V. globator*, *V. perglobator* and *V. tertius*. On the other hand, *Volvox* species with rapid light-independent divisions and slow light-dependent divisions usually coexist in the lower latitudes of both hemispheres (between 52-57° N and 35-36° S).

The family Volvocaceae, for which there are no reliable paleontological data, originated, according to a multigene data set (Herron *et al.* 2009), at least 180 million years ago (MYA). Consequently, the evolution of *Volvox* and other colonial volvocine algae had occurred predominantly under the warm climate of Jurassic, Cretaceous, and considerable part of Cenozoic (DeConto *et al.* 2008, Eldrett *et al.* 2009, Pross *et al.* 2012). Even during winter and fall (under conditions of short daylight periods) at relatively high paleolatitudes in both Northern and Southern Hemispheres, the temperature might have been favorable for the growth and development in algal populations of the genus *Volvox*. For example, there are published data (Poole *et al.* 2005, Pancost *et al.* 2013) that the coldest month mean temperature at paleolatitudes 55-62° S was, as a rule, about + 10° C. It is appropriate to note in this connection that such a temperature is suitable for natural growth and reproduction of *V. aureus* and *V. globator* in temperate latitudes of the USA (Senft *et al.* 1981). Therefore, there is reason to believe that the above-mentioned evolutionary reorganizations in the ontogenesis of *Volvox* (carried out by the changes in rate, diurnal rhythm and light-dark control of gonidial cleavage) might have occurred as adaptations to short winter and fall days in relatively high latitudes under conditions of warm climate in the deep past. This suggestion (Desnitskiy 2016) may explain why the series of rapid and light-independent cell divisions slowed down during the process of evolution in several members of the genus *Volvox* and became dependent on light.

As mentioned above (Herron *et al.* 2010), the major ontogenetic transition concerning the control of gonidial cleavage had evolved in three evolutionary lines of *Volvox* and represents a homoplasy. A preliminary hypothesis may be very cautiously suggested only for one of these lines, leading to *V. tertius* and *V. dissipatrix*. In trying to figure out where the early evolution of this line might have occurred, it is important to bear in mind a few circumstances. First, *V. dissipatrix* is characterized by limited geographical distribution (Australia, India, Philippines) and does not occur in temperate latitudes and subtropics of the Northern Hemisphere, whereas *V. tertius* is more widespread and occurs in both hemispheres and on several continents, including Australia and South Asia. Second, according to published multigene data set (Herron *et al.* 2009), the ontogeny transformations that led to the change of gonidial cleavage process in the evolutionary line, including *V. dissipatrix* and *V. tertius*, had occurred between about 45 and 60 MYA (i.e., during early Cenozoic Era, probably in Paleocene or early Eocene Epoch). Third, according to published data on continental drift in the past (e.g., Veevers *et al.* 1991, Scotese 2001), Australia was partly in relatively high latitudes of the Southern Hemisphere during early Cenozoic. Such an analysis (Desnitskiy 2016) represents an endeavor to shed some light on ecological and geographical aspects of the evolution of *Volvox* and its ontogeny.

Earlier discussion has dealt so far with the evolution of asexual developmental cycles in *Volvox*. As a matter of fact, the asexual reproduction plays extremely important role in the life of natural populations of colonial volvocine algae. Moreover, many publications considering the evolutionary trends in the Volvocaceae (e.g., Kirk 1998, 2005, Desnitskiy 2008a, Herron *et al.* 2010, Olson and Nedelcu 2016) have preponderantly used data on their asexual development and reproduction. However, further elaboration of our concept of ecological evolution of ontogeny in the genus *Volvox* would require the use of data concerning dispersal and extinction of these algae. In this connection some information about their zygotes might be used as a starting point. The sexual life cycle of *Volvox* and other colonial Volvocaceae includes a stage of thick-walled and dormant zygospore (zygote) which is able to survive unfavorable conditions, being resistant to desiccation and freezing. Recently published ideas of Annette Coleman are very important in this respect. "Zygotes should be superb emigrants. The vectors responsible for their transportation to both near and distant sites are probably waterfowl, whose most common migration routes may play some part" (Coleman 2012, p. 506). Let us also remind that the general topic of waterbird-mediated dispersal of aquatic organisms exists in contemporary ecology (e.g., Santamaria and Klaassen 2002).

An important point is that extant groups of birds had been already represented in early Cenozoic (Jarvis *et al.* 2014, Brusatte *et al.* 2015). On the other hand, emergence of long

distance bird migrations might have taken place as early as the middle Eocene (i.e., probably around 45 MYA) (Louchart 2008). Consequently, it is reasonable to admit that in the absence of migrating birds, early Cenozoic flora of colonial volvocine algae did not include species with wide distribution (simultaneously on several continents). Probably it was represented by species with local distribution; many of them later died out leaving no fossil records. It may be also remarked that in the warm and humid climate of early Cenozoic Era, the zygotes should have played a lesser role for both survival and dispersal of the colonial Volvocaceae than today. This paragraph shows an attempt to reconstruct peculiar conditions, under which the evolutionary transformations of gonidial cleavage process in several members of the genus *Volvox* might have occurred in the deep past.

Returning to the extant *Volvox* species, it is of interest to note that *V. aureus* (the sole cosmopolitan member of the genus) is represented not only by strains with sexual reproduction and zygospore formation, but also by strains, in which males are absent or extremely rare. In old cultures of such strains, many gonidia are transformed into orange parthenospores, which are presumed to be haploid, but have the same appearance as mature zygotes (e.g., Starr and Zeikus 1993, Desnitskiy 2002). They seem to be also important for survival and dispersal (similar to dormant zygotes). The parthenosporic strains are poorly investigated and they have not been recorded so far in other *Volvox* species. Finally, it is appropriate to refer to Maynard Smith's (1978) monograph on the evolution of reproductive processes in both plants and animals. He noted that species, which lost the capacity for sexual reproduction, are frequently characterized by more wide distribution, though they have limited evolutionary perspectives.

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