Review

A Review on the Evolution of Development in *Volvox* – Morphological and Physiological Aspects

Alexei G. Desnitski

Biological Institute of St. Petersburg State University, St. Petersburg, Russia

SUMMARY

This paper presents a morphophysiological concept of the evolution of *Volvox* development. We use published data concerning differences in size of the mature gonidia, rates of their division and peculiarities in segregation of somatic and reproductive cell lines. Based on this, four programmes (types) of asexual development of *Volvox* are recognized, and the evolutionary relationships among these programmes (but not among any concrete species of *Volvox*) are elucidated. The first developmental programme (*Volvox powersii* – *V. pocockiae*) is clearly primitive for the genus. This programme is characterized by ancestral features: large gonidia, division is fast, and there is no unequal (asymmetric) division into two cellular types. The second developmental programme(*V. carteri*), the third programme (*V. tertius*) and the fourth programme (*V. aureus*) are all derived, but constitute different phylogenetic trends. They each have some derived features: the second programme involves asymmetric division, the third programm involves slow division, while the fourth programme involves small gonidia and slow division. The evolutionary concept is supplemented by data on sexual reproduction in various species of *Volvox*.

Introduction

The volvocine green flagellates – *Chlamydomonas, Gonium, Pandorina, Eudorina, Pleodorina and Volvox* – have long attracted the interest of evolutionary biologists [1, 2, 4, 21, 68]. The phylogeny of the colonial Volvocales currently attracts attention of morphologists [18, 20, 39–41, 65] as well as geneticists and molecular biologists [3, 25, 27, 28, 33, 48, 49]. The phylogenetic relationships among various colonial Volvocales are more complicated than once imagined, and the genera *Gonium, Pandorina, Pleodorina* and *Volvox* do not represent a sequential evolutionary series as has been supposed [33, 62].

Besides morphological, genetic and molecular approaches, a physiological approach is also relevant. Using this approach, I have been able to elucidate cellular mechanisms of the evolution of ontogenesis and some trends in the evolution of multicellularity in *Volvox* [13, 14]. The present paper deals with a further clarification of the problem. First, the taxonomy and phylogeny of *Volvox* are considered. Then a comparative survey of cell division pattern is presented. In con-

clusion, I present a morphophysiological concept of the evolution of *Volvox* development.

Taxonomy and Phylogeny

The genus *Volvox* includes at least 18 recognized species and can be divided into 4 taxonomic sections which are distinguished by the shape of somatic cells, presence or absence of cytoplasmic bridges, the size of mature gonidia and the structure of the extracellular matrix [13, 26, 56, 59]. A historical survey of *Volvox* taxonomic research may be found in Smith's article published in 1944 [56]. At the beginning of this century, Shaw [50–54] divided the genus *Volvox* into several closely related genera (divergent evolution). Later these new taxa were reduced by other researchers [46, 56] to the rank of the taxonomic sections of a single genus, *Volvox*. Smith's classification [56] is currently recognized [12, 13, 26, 33, 38, 40, 47, 59, 67], and the list of the sections and species of *Volvox* which is given below differs slightly from that in Smith's survey: a new species, *V. pocockiae* discovered by Starr

[59], is added, and *V. weismannia* is excluded; the latter is now regarded as *V. carteri* f. *weismannia* [30, 38, 58].

The section Merrillosphaera includes *Volvox africanus, V. carteri, V. gigas, V. obversus, V. powersii, V. spermatosphaera* and *V. tertius.*

The section Janetosphaera includes *V. aureus* and *V. pocockiae.*

The section Copelandosphaera includes only one species, *V. dissipatrix.*

The section Euvolvox includes *V. amboensis, V. barberi, V. capensis, V. globator, V. merrillii, V. perglobator, V. prolificus* and *V. rousseletii.*

More detailed information about characteristics of various sections and species of *Volvox* may be found elsewhere [13, 26, 36–38, 43–45, 56, 58–60, 63, 67].

Some ideas concerning the phylogenetic position of several species have been published [5, 22, 29, 67]. *V. gigas* and *V. powersii* are argued to be the most primitive members of the genus *Volvox*. Both have many characteristics of structure and development in common with the genus *Pleodorina* [5, 67]. A mutant of *V. powersii* is morphologically indistinguishable from *Pleodorina californica* [67]. *V. carteri* and *V. obversus* are considered to be more advanced species of *Volvox* [22, 29]. Both demonstrate unique characters in the process of gonidial differentiation. On the other hand, in a paper published more than 40 years ago [5], Cave and Pocock considered the Euvolvox species to be the most advanced in the genus. Their point of view was based on the differences in the general morphology of spheroids as well as in the chromosomal numbers: the species of the Euvolvox section are characterized by 5 chromosomes, whereas the species in other sections have 12–16 chromosomes (see [5, 6, 42] for the haploid numbers of chromosomes).

For a long time, however, there were different ideas about evolution of *Volvox*. In 1918 Crow [10] thought that all species of *Volvox* (which were known at the beginning of the century) arose from the genus *Haematococcus* independently of other colonial Volvocaceae (*Gonium – Pleodorina* series). A decade later [15, 16], Fritsch (who was Crow's teacher) allied with *Haematococcus* only those *Volvox* species which have stellate somatic cells (Euvolvox section). He considered other species of *Volvox* to be members of the traditional colonial volvocine series. Most of Fritsch's contemporaries did not share his point of view of the polyphyletic origins of *Volvox*. In 1984, however, Fritsch's ideas received strong support from Hoops's work [20] on the comparative analysis of the flagellar apparatuses in *V. carteri* f. *weismannia* (Merrillosphaera section) and *V. rousseletii* (Euvolvox section).

Recent analysis of ribosomal RNA sequences in 12 volvocalean flagellates [33, 49] has also favoured the polyphyletic origins of *Volvox*. The family of the green colonial Volvocaceae (including the genera *Pleodorina, Eudorina, Pandorina, Gonium, Platydorina, Volvulina*), however, represents a monophyletic group, which originated about 50 million years ago. The evolutionary trends within the family are far from being fully elucidated. According to the molecular studies (see especially Fig. 2 in [49], p. 203), there are two main branches in the phylogenetic tree of the Volvocaceae. The first branch includes *Pleodorina californica, Volvox aureus, V. carteri* and *V. obversus*, whereas *Gonium pectorale, Eudorina elegans, Platydorina caudata, Pandorina morum* and *V. capensis* are in the second branch. Both branches are closely related with the unicell *Chlamydomonas reinhardtii*, but they are at a significant phylogenetic distance from another volvocine unicell, *Haematococcus lacustris*. The comparative analysis of ribosomal RNA sequence by Buchheim and Chapman [3] also demonstrates that *V. aureus* and other colonial genera (except *Stephanosphaera*) cannot be allied with *Haematococcus*.

Thus recent molecular data strongly favour Fritsch's [15, 16] and Hoops's [20] ideas about the polyphyletic origins of the genus *Volvox*. The ideas that all [10] or some [15, 16] species of *Volvox* might be closely related to *Haematococcus* are not substantiated.

A regA⁻/gls⁻ double mutant of *V. carteri* f. *nagariensis* results in the formation of an organism with only one cell type resembling *Eudorina* [28, 64]. There is also a mutant converting *V. powersii* to a *Pleodorina* phenotype [67]. In this connection the idea that "the different levels of developmental and organization complexity that characterize various extant volvocacean genera may represent alternative stable states, among which there may have been multiple transitions during the phylogeny of this group" (Larson, Kirk, and Kirk [33], p. 102) is relevant. It is possible that volvocacean taxa which are currently recognized represent grades of organizational and developmental complexity, rather than phylogenetic clades of closely related organisms. Therefore, some volvocacean species (e.g., some representatives of *Eudorina*, some representatives of *Pleodorina*, etc.) might have originated from various *Volvox* species by means of mutations which reduced their organization [33].

On the other hand, recent morphological investigations [41] have proposed a new genus, *Yamagishiella* Nozaki, intermediate between *Pandorina* and *Eudorina*. Besides, it has been suggested [39] that the genus *Gonium* should be transferred from the family Volvocaceae to the family Goniaceae Pascher which comprises two genera, *Gonium* and *Astrephomene*. Finally, a cladistic analysis based on morphological data on 25 species of volvocalean flagellates has been undertaken to deduce the phylogenetic relationships within the colonial Volvocales [40]. It is appropriate to note that the study involved four species of *Volvox* belonging to the four sections: *V. aureus* (Janetosphaera section), *V. carteri* (Merrillosphaera section), *V. dissipatrix* (Copelandosphaera section) and *V. rousseletii* (Euvolvox section). The results demonstrate that *Volvox* is a monophyletic genus. Nozaki and Itoh claim that "species of *Volvox* may be considered closely related to one another irrespective of their morphological diversity in vegetative colonies" (see [40], p. 361). Certainly, recent works of Nozaki's group [39, 40] can

hardly be reconciled with the recent data on molecular phylogeny [3, 33, 49] and with previous morphological investigations [15, 16, 20]. Concluding the taxonomic and phylogenetic discussion, it should be noted that the situation is unstable and new molecular, morphological and physiological approaches in the future can be expected to lead to further revisions of volvocacean taxonomy and phylogeny.

Comparative Analysis of Cell Division Courses

There are two principal types of asexual development in the genus *Volvox* [6, 13, 30, 59, 60]. In all members of the section Merrillosphaera, and in *Volvox pocockiae* (belonging to Janetosphaera section), the extended period of gonidial enlargement (up to 30–90 μm in diameter) is followed by a series of gonidial cleavage divisions in the absence of growth. The second developmental pattern is observed in *V. aureus* (the second species of the Janetosphaera section), *V. dissipatrix* (the only representative of the Copelandosphaera section), and all members of the section Euvolvox; the mature gonidia are relatively small (up to 15–25 μm in diameter) and the cells grow during the intervals between divisions.

Biochemical investigations of the asexual life cycles of *V. carteri* and *V. aureus* are in accord with the concept that these two species have different patterns of development. In *V. carteri* RNA and proteins are most actively synthesized in the gonidia during their growth, but both transcription and translation are considerably depressed during the series of rapid divisions [30]. By contrast, in *V. aureus* RNA synthesis is minimal during gonidial growth and maximal during gonidial cleavage [66]. Nevertheless, nuclear DNA replication in both species occurs only during the intervals between consecutive gonidial divisions: each mitosis is preceded by the doubling of the amount of nuclear DNA [9].

In the protistological literature [55] the term "palintomy" is sometimes used to designate the process during which a giant parental cell undergoes a rapid sequence of repeated divisions, without intervening growth. This process produces numerous small cells. In *Volvox*, palintomy occurs in *V. carteri* [13, 30, 58, 60], *V. pocockiae* [59], *V. obversus* [22], *V. gigas* and *V. powersii* [67]. These species are characterized by large gonidia, division without growth, and by a rapid rate of gonidial cleavage. The interval between two consecutive divisions is an hour or less at 20–30 °C. On the other hand, in *V. aureus* and other species with small gonidia there is no palintomy during the asexual life cycle and the interval between two consecutive divisions in the *V. aureus* gonidium is about four hours at 22–24 °C [13].

I have addressed recently the problem of the evolutionary relationship between the palintomic (e. g., *V. carteri*) and the nonpalintomic (e. g., *V. aureus*) types of the asexual life cycles in *Volvox* [13]. In addressing this, a number of facts were taken into account. First, the extensive literature on asexual reproduction of unicellular *Chlamydomonas reinhardtii* [8, 19, 35, 57] and the colonial volvocacean genera *Pandorina, Eudorina, Pleodorina,* etc. [6, 7, 17, 23, 24, 34] clearly demonstrates that all of these organisms are palintomic. Secondly, *V. powersii* and *V. gigas*, perhaps the most primitive species of *Volvox* [67], are also characterized by palintomy. Thus it appears certain that the palintomy exhibited by *V. carteri* is a primitive feature of the family Volvocaceae and that the pattern of development exhibited by *V. aureus* is derived. However, these two species belong to different taxonomic sections of the genus *Volvox* (Merrillosphaera and Janetosphaera). The evolutionary relationships between these sections are obscure. It is of particular importance to

Table 1. Comparative aspects of asexual development in three species of *Volvox*

Character	*V. carteri*	*V. aureus*	*V. tertius*
1. Fraction of the asexual life cycle occupied by the process of cleavage	∼0.2	∼0.6	∼0.4
2. Size of gonidia at the onset of cleavage	50–60 μm	20–25 μm	42–45 μm
3. Presence or absence of cell growth between consecutive divisions	no growth	growth	no growth
4. Cell cycle duration (interval between divisions) at 22–24 °C	∼1 h	∼4 h	∼3 h
5. Is light required for cleavage to continue?	no	yes	yes
6. When does a series of divisions start? (16 h light/8 h dark regime)	during the second half of the light period	during the beginning of the light period	during the beginning of the light period
7. Relative resistance of cleavage to inhibitors of RNA and protein synthesis	high	low	high
8. Relative resistance of cleavage to inhibitors of DNA synthesis	high	low	low

note that although Starr [59] places *V. pocockiae* in the section Janetosphaera with *V. aureus, V. pocockiae* is characterized by the *V. carteri* type of asexual development. This reinforces the concept that the reduced palintomy of *V. aureus* is a derived trait. Thus, *Volvox* – the whole genus or even separate sections of it – may be used as an excellent model for analyzing the cellular and molecular mechanisms that underlie ontogenetic evolution.

Elsewhere [13] an attempt was made to quantify some of the cellular parameters involved in the evolution of asexual ontogenesis in *Volvox* using comparative and physiological approaches. Three species were studied. Clonal cultures of *V. aureus* and *V. tertius* (the homothallic strains P-I and V-3 respectively) originated from material found in the St. Petersburg region. Zygotes of *V. carteri* f. *nagariensis* made by crossing the female strain HK-10 and the male strain 69-1b were obtained from the University of Texas Culture Collection of Algae. I germinated the zygotes, recovered the male and female strains from the progeny and used the female strain in the following work. The results are briefly summarized in Table 1.

Comparison of ontogenetic characters in *V. carteri* and *V. aureus* shows that the palintomic reduction in the latter species is connected with several changes in cellular behaviour. There has been a shortening of the gonidial growth period accompanied by a marked slowing of the tempo of the gonidial cleavage divisions and pronounced growth of the cells during the long intervals between consecutive divisions. Moreover, the light/dark control of development is changed in two ways: the moment of cleavage initiation has been shifted from the second half of the light period to its beginning, and continuation of cell division has become light-dependent. In *V. aureus* the rate of RNA and protein synthesis is maximal not during gonidial growth as in *V. carteri* but during the series of divisions. A similar trend appears to characterize the dynamics of the intracellular pools of DNA precursors, since inhibitors of deoxynucleotide synthesis block gonidial cleavage of *V. aureus*, but not that of *V. carteri*.

Interestingly, previous studies [13] of the asexual development of *V. tertius* suggest that palintomic reduc-

tion may be discovered within the Merrillosphaera section as well, presumably having arisen independently of the evolutionary changes within the Janetosphaera section. Only some palintomic traits are reduced in *V. tertius*. Some features of its asexual development are similar to those of *V. aureus*, but the others are more similar to *V. carteri* (see Table 1). The occurrence of large gonidia cleaving without cellular growth is not necessarily accompanied by a rapid rate of division. It may be supposed that the programme of asexual development of *V. tertius* is a modification of the palintomic programme. However, in the *V. tertius* programme there seems to be no provision of an endogenous pool of DNA precursors in the gonidium at the beginning of cleavage. Thus the data on the analysis of rates, diurnal rhythms and light/dark control of cell divisions in *V. carteri* f. *nagariensis, V. aureus* and *V. tertius*, along with the data obtained in experiments with metabolic inhibitors, demonstrate the occurrence of specific physiological characters in each species.

A Concept of Morphophysiological Evolution – Four Developmental Programmes in *Volvox*

First of all, it is appropriate to recollect that *Volvox carteri* and *V. obversus*, the two palintomic species of the Merrillosphaera section that are believed to be evolutionarily advanced [22, 29], are characterized by the segregation of presumptive reproductive and somatic cells at relatively early stages of cleavage – during transition from 16 or 32-celled stage to 32 or 64-celled stage. But in all other species of *Volvox* – including all other members of the Merrillosphaera section – gonidia become morphologically different from somatic cells only after completing the processes of cleavage or inversion [47, 56]. Therefore, there is a possibility for further elaboration of concepts regarding the evolution of *Volvox* ontogeny (at least within the sections Merrillosphaera and Janetosphaera). Based on differences in size of the mature gonidia, rates of cleavage, and spatial patterns of cleavage, one can delineate four cellular programmes of asexual development in *Volvox* (see Table 2).

Table 2. Cellular programmes of asexual development of *Volvox*

Programmes of development and the typical species	Size of mature gonidia and presence/absence of growth	Rate of division	Presence or absence of asymmetric division
The first programme (*V. powersii, V. gigas, V. pocockiae*)	large, cleave without growth	fast	equal division only
The second programme (*V. carteri, V. obversus*)	large, cleave without growth	fast	asymmetric division
The third programme (*V. tertius*)	large, cleave without growth	slow	equal division only
The fourth programme (*V. aureus, V. globator*)	small, grow between divisions	slow	equal division only

The first developmental programme is characteristic of *V. powersii, V. gigas* and *V. pocockiae*. These species have large gonidia, division is fast, and there is no unequal (asymmetric) division into two cellular types. The same programme is characteristic of colonial genera such as *Pandorina, Eudorina* and *Pleodorina* [6, 7, 17, 23, 24, 34, 41], suggesting that this is the primitive developmental programme of the volvocacean algae.

The second developmental programme is characteristic of *V. carteri* and *V. obversus*. It differs from the first programme in one point only: there are asymmetric divisions during cleavage, forming the anlagen of the presumptive reproductive and somatic cells of the next generation. This is clearly a derived feature [22, 29] not found in any other Volvocaceae [17, 24, 41, 62].

The third developmental programme is characteristic of *V. tertius* which has large gonidia dividing without growth (similar to other members of the section Merrillosphaera), but slow cleavage, and no unequal division or visible segregation of cell lines during cleavage.

The fourth developmental programme is characteristic of *V. aureus*, although in all features yet studied it resembles the developmental programme of *V. dissipatrix*, the only species of the section Copelandosphaera, and all species of the section Euvolvox. This programme involves relatively small gonidia that cleave slowly, without asymmetric division, and with growth between successive divisions. My unpublished results on *V. globator* (strain No 955 from the University of Texas Culture Collection of Algae) show that the interval between two consecutive divisions occupies about three hours at 24 °C and placing the spheroids with 2–8-celled gonidia in darkness blocks utterly subsequent cell divisions (similar to the experiments with *V. aureus*).

I shall now proceed to the evolutionary relationships among these four programmes of *Volvox* development (but not among any concrete species or sections of the genus). Such an unusual approach seems to be relevant in this case, because, as it has been shown above, recent morphological [40] and molecular [33, 49] studies of the phylogenetic relationships among various sections and species of *Volvox* gave contradictory results. As noted earlier, the first developmental programme (*V. powersii* – *V. pocockiae*) is clearly ancestral for the group. The second developmental programme (*V. carteri*) and the third programme (*V. tertius*) are both derived, constituting two different phylogenetic trends within the Merrillosphaera section. At last, the fourth developmental programme appears within the Janetosphaera section (*V. aureus*). Developmental programmes similar to that in *V. aureus* appear to be present in poorly investigated species of two other sections (Copelandosphaera and Euvolvox) but their relationship to the *V. aureus* programme is obscure, because of the possible polyphyletic nature of the genus [16, 20, 33, 49].

Only the first and second developmental programmes are palintomic, whereas the third and fourth developmental programmes are characterized by changes in the light/dark control of cell division and by changes in the control of DNA synthesis. The fourth developmental programme also differs from the others in regards to the dynamics of RNA and protein synthesis during the asexual life cycle. It is an additional argument supporting the idea that this programme is the most derived in the evolutionary respect.

Finally, it should be noted that the large gonidia dividing without growth, which are characteristic of the first, second, and third developmental programmes, are correlated with both rapid and slow tempo of divisions, and with both the presence and absence of asymmetric division and segregation of cellular lines during cleavage. In contrast, a small size of mature gonidia, characteristic of the fourth developmental programme (*V. aureus*), is encountered only with a slow cleavage, without visible segregation of cell lines. It is another argument supporting the idea that the small gonidial size is an evolutionarily advanced trait.

Final Remarks

The concept of the morphophysiological evolution of *Volvox* development presented here is based mainly on data about cellular reproduction during asexual life cycle. It is possible, however, to incorporate some additional data on sexual reproduction. In most species of *Volvox* (e.g., *V. carteri, V. gigas, V. pocockiae, V. rousseletii*), the process of zygote germination results in the liberation of a haploid biflagellated zoospore which, by cleavage and inversion, forms a small asexual spheroid [38, 44, 58, 59, 61, 67]. In contrast, in *V. tertius* and *V. aureus* cell division and inversion occur under the protection of a zygote wall with the release of a miniature spheroid rather than a unicellular zoospore [11, 45]. This development seems to be more advanced in the evolutionary respect, and this is an additional argument supporting the idea that *V. tertius* and *V. aureus* are the derived species (in the Merrillosphaera and Janetosphaera sections, respectively).

The mature zygotes of all species of *Volvox* are of rather large size due to a prolonged growth of the eggs before or after fertilization [56]. Moreover, Darden's work [11] shows that during zygote germination of *V. aureus*, cell divisions appear to occur without cellular growth. Though nothing is known about the rate of this process, the data may be interpreted in support of retaining a number of palintomic traits in sexual reproduction. On the other hand, the evidence of Pocock's work [44] shows that in the course of zoospore development in *V. rousseletii*, each interval between two consecutive divisions lasts about an hour or a bit less, and no cellular growth occurs during this rapid cleavage.

The palintomic traits of development after zygote germination seem to be retained rather than lost during the process of evolution because in the absence of somatic cells they are necessary for surviving. This offers

additional support to the idea that palintomic reduction, which is characteristic of the asexual development in several species of *Volvox*, is the result of a peculiar evolution of organisms which are already at a multicellular level of organization. It is appropriate to recollect that the differentiation into a small number of reproductive cells and numerous biflagellate somatic cells guarantees motility throughout the asexual life cycle of *Volvox*. It is, beyond doubt, an important advantage compared to many other colonial Volvocales, such as *Gonium, Pandorina, Yamagishiella, Eudorina* [1, 12, 31, 32, 49]. In this connection it may be hoped that future taxonomic revisions of the family Volvocaceae or the genus *Volvox* will not deny the thesis that the non-palintomic type of *Volvox* asexual development is derived. It should be emphasized again that palintomy has apparently been reduced in parallel (and to various extent) in different sections and species of *Volvox*.

In concluding, I agree with the recent molecular study [33] suggesting origins of some representatives of the genera *Pandorina, Eudorina, Pleodorina*, etc. from some species of *Volvox*. I think, however, that only the palintomic species of *Volvox* (like *V. powersii* or *V. carteri*) had been capable to undergo such a "degenerative" evolution. From the morphophysiological point of view, I doubt if the palintomic volvocacean species, such as *Eudorina elegans, Pandorina morum* or *Platydorina caudata*, might have originated from the Euvolvox section, the members of which are characterized by small gonidia and cellular growth during the prolonged intervals between consecutive divisions.

Acknowledgements

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Alexei G. Desnitski, Biological Institute of St. Petersburg State University, Oranienbaumskoye sch. 2, Stary Peterhof, St. Petersburg, 198904, Russia