

ALGAE – ВОДОРОСЛИ

Problems of species and the features of geographical distribution in colonial volvocine algae (Chlorophyta)

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Abstract. More than ten new species of colonial volvocine algae were described in world literature during recent years. In present review, the published data on taxonomy, geographical distribution and the species problem in this group of algae, mainly from the genera *Gonium*, *Pandorina*, *Eudorina*, and *Volvox*, are critically discussed. There are both cosmopolitan volvocalean species and species with local or disjunct distribution. On the other hand, the description of new cryptic taxa in some genera of the colonial family Volvocaceae, such as *Pandorina* and *Volvox*, complicates the preparation of a comprehensive review on their geography.

Keywords: *Gonium*, *Pandorina*, *Volvox*, cryptic taxa, reproductive isolation, volvocalean geography.

Проблемы вида и особенностей географического распространения у колониальных вольвоксовых водорослей (Chlorophyta)

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Резюме. В последние годы в мировой литературе описано более десяти новых видов колониальных вольвоксовых водорослей. В настоящем обзоре критически обсуждаются опубликованные данные по таксономии, географическому распространению и проблеме вида в этой группе водорослей, главным образом из родов *Gonium*, *Pandorina*, *Eudorina* и *Volvox*. Существуют как космополитные виды вольвоксовых, так и виды с локальным или дизъюнктивным распространением. С другой стороны, описание новых криптических таксонов в некоторых родах семейства Volvocaceae, таких как *Pandorina* и *Volvox*, усложняет подготовку всестороннего обзора по их географии.

Ключевые слова: *Gonium*, *Pandorina*, *Volvox*, география вольвоксовых, криптические таксоны, репродуктивная изоляция.

Among the green algae (Chlorophyta), which play an important role in freshwater ecosystems, one of the groups most often attracting the attention of researchers is the colonial green flagellates from the families Volvocaceae Ehrenb. (as revised by Nozaki, Kuroiwa, 1992), Goniaceae (Pascher) Pascher and Tetrabaenaceae Nozaki et Mot. Itoh. This group of algae, including about 60 species, is studied in relation to evo-

lution, cell differentiation, morphogenesis and genomics (Herron *et al.*, 2009; Umen, Olson, 2012; Matt, Umen, 2016; Featherston *et al.*, 2018). However, the problem of their geographical distribution attracts attention much less often. Probably this may be partly explained by the fact that their taxonomy is in a sorry condition. As noted in a recent review (Herron, Nedelcu, 2015: 137), “genus-level taxonomy within the Volvocales is badly in need of revision, as most nominal genera are polyphyletic. It is hard to give an exact number of volvocine species, since many described species are almost certainly synonymous”. Many recent phylogenetic studies of the colonial volvocine algae are based on the sequence data of five chloroplast genes (Herron, Michod, 2008; Nozaki *et al.*, 2014, 2015a, 2019a). Phylogenetic trees are gradually modified after the description of new taxa. These works indicate, however, that the family Volvocaceae, taken as a whole, is monophyletic, whereas the genera *Volvox* L., *Pleodorina* W. Shaw, *Eudorina* Ehrenb., *Pandorina* Bory and *Volvulina* Playfair are not (Nakada, Nozaki, 2015; Nanjundiah *et al.*, 2018). In particular, the genus *Volvox* is represented by at least three, but probably four separate evolutionary lineages (Herron *et al.*, 2010).

Significant generalizations in the field of biogeography and the closely related problem of species structure were achieved as a result of studies only on very few representatives of the colonial volvocaceans – primarily *Pandorina morum* (O. F. Müll.) Bory (Coleman, 1959, 1977, 2001). Besides, in recent years a number of new taxa of the colonial volvocine algae were described and the publication of such articles (Isaka *et al.*, 2012; Nozaki *et al.*, 2014, 2015a, 2019b) changed former ideas concerning the geographical distribution of several species. This essay represents an attempt to synthesize literature data on the species problem, geographical distribution, and some features of the developmental cycles of *Volvox* and other related genera.

Brief survey of the colonial volvocine algae and their geographical distribution

There are more than a thousand species of freshwater green algal flagellates (mostly unicells) that are traditionally assigned to the order Volvocales sensu Nakada, Misawa and Nozaki (Nakada *et al.*, 2008) (sometimes referred to as Chlamydomonadales F. E. Fritsch). The present paper deals only with a relatively small group (hardly more than 60 species) of colonial volvocaceans belonging to the families Tetrabaenaceae, Goniaceae and Volvocaceae (TGV-clade according to Herron, Michod, 2008; Herron *et al.*, 2009). It should be remarked that there are also a few primitive colonial species in the distantly related volvocalean families Haematococcaceae G. M. Sm. and Spondylomoraceae Korshikov, but they extremely rarely attract the attention of researchers (Nakada *et al.*, 2010; Sugasawa *et al.*, 2015; Munakata *et al.*, 2016). They are usually not considered in the general context of colonial Volvocales (Nozaki, Itoh, 1994; Nozaki *et al.*, 2014; Herron, Nedelcu, 2015). Therefore, the data on these two families are beyond the scope of present paper.

The brief information on colonial volvocine genera (the TGV-clade) is represented in Table 1.

Table 1

Basic data on colonial volvocine algae

Family	Genus	Species number	Cell number in asexual colony
Tetrabaenaceae	<i>Basichlamys</i>	1	4
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Goniaceae	<i>Gonium</i>	10	8, 16 or 32
	<i>Astrephomene</i>	2	32 or 64
Volvocaceae	<i>Pandorina</i>	6	8 or 16
	<i>Volvulina</i>	4	8 or 16
	<i>Yamagishiella</i>	1	16 or 32
	<i>Platydorina</i>	1	16 or 32
	<i>Colemanosphaera</i>	2	16 or 32
	<i>Eudorina</i>	9	16 or 32
	<i>Pleodorina</i>	6	16, 32, 64 or 128
	<i>Volvox</i>	23	500, 1000 or more (up to 50000)

All these algae are haplonts, with the zygote as the sole diploid stage. The colonies of *Basichlamys* Skuja, *Tetrabaena* From. and *Gonium* O. F. Müll. have the form of flat or slightly curved plates, while *Astrephomene* Pocock and all volvocacean genera (except *Platydorina* Kof.) have spherical colonies. *Platydorina* initially develops as a spheroid, but is secondarily flattened. Differentiation into somatic and reproductive cells is characteristic only of the genera *Astrephomene*, *Pleodorina* and *Volvox*. The Table 1 encompasses data from recent papers (Nozaki *et al.*, 2006, 2014, 2015a, 2019a, 2019b; Coleman, 2012; Herron, Nedelcu, 2015). According to the recent data (Pröschold *et al.*, 2018), however, it cannot be excluded that the family Tetrabaenaceae represents a separate evolutionary lineage. As noted above, numbers of species within several genera may be approximations, because the validity of some described species is questionable.

Many colonial volvocine species were described during last 30 years by Hisayoshi Nozaki and his colleagues. During 1990^s, new volvocine taxa (species and genera) were established primarily on the basis of morphological characters (at both light- and electron-microscopic levels) (e. g., Nozaki, Kuroiwa, 1992; Nozaki, Itoh, 1994). However, later the fact of limited value of morphological characters alone became apparent. It was shown that the data on the sequences of the second internal transcribed spacer of the nuclear ribosomal gene cistron (ITS-2) are very useful for characterizing populations and species, as well as for establishing the boundaries of species (Mai, Coleman, 1997; Fabry *et al.*, 1999; Coleman, 2001, 2002, 2009). Therefore, after 2000, both molecular and morphological criteria were used together to describe new taxa of colonial volvocine algae: five species of *Volvox* (Nozaki, Coleman, 2011; Isaka *et al.*,

2012; Nozaki *et al.*, 2015a, 2019b), two species of *Pleodorina* (Nozaki *et al.*, 2006), two species of *Eudorina* (Nozaki, Krienitz, 2001; Nozaki *et al.*, 2019a), a species of *Gonium* (Hayama *et al.*, 2010) and *Colemanosphaera* Nozaki, a new genus with two species (Nozaki *et al.*, 2014).

I will now proceed to discuss some features of the geographical distribution of colonial volvocine algae. Useful information on this issue can be found in a monograph by Ettl (1983). It would be advisable to update this information in the light of the aforementioned articles of recent years on colonial Volvocales. However, this seems to be difficult due to an unsatisfactory state in the taxonomy of this group (as noted above). Therefore, it is reasonable to consider only current data on selected algal species from the Volvocaceae family, as well as from closely related genus *Gonium*.

Colonial *Gonium pectorale* O. F. Müll., *Pandorina morum*, and *Eudorina elegans* Ehrenb. can be considered cosmopolitan, since all these algae are widely distributed in fresh waters on six continents (Iyengar, Desikachary, 1981; Ettl, 1983; Parra *et al.*, 1983; Nakada, Nozaki, 2015; etc.). They were also reported from the Arctic (Sheath, Steinman, 1982). More detailed information on the species problem and biogeography of *Gonium pectorale*, *Pandorina morum*, and *Eudorina elegans* will be represented in the next section. It is worth noting here that *Platydorina caudata* Kof. was recorded on four continents (North America, South America, Europe and Asia), but the monotypic genus *Platydorina* is a characteristic representative of freshwater phytoplankton only in the Midwestern United States, and in other places this alga is extremely rare (Coleman, 1996).

I am next to consider the geographical distribution of *Volvox*, which was enigmatic from Ettl's (1983) point of view. Such an opinion, apparently, was based on the fact that this genus encompasses species with a very wide distribution and species with a local distribution in various parts of the world. Some *Volvox* species are almost certainly absent on some continents. Below I updated Ettl's data on the geography of *Volvox* to reflect new taxonomic publications (Desnitskiy, 2016), as well as data on the ecological and physiological diversity of this genus of algae (Desnitski, 1995; Herron *et al.*, 2010).

Volvox aureus Ehrenb. is the only cosmopolitan representative of the genus, widely distributed on six continents (Smith, 1944; Iyengar, Desikachary, 1981; Ettl, 1983; Parra *et al.*, 1983). *Volvox globator* L. was also recorded on six continents, but in Africa, it was found only in the phytoplankton of the Nile River system in Egypt (Talling *et al.*, 2009). *V. tertius* Art. Mey. was recorded on five continents (it was not reported from Africa) (Desnitskiy, 2016). These three most common *Volvox* species are homothallic (sexual reproduction is possible within a clone) (Starr, Zeikus, 1993). On the other hand, there are species with local distribution (on one continent) and they may be homothallic (e. g., *V. ferrisii* N. Isaka, Matsuzaki et Nozaki, *V. kirkiorum* Nozaki, Kawai-Toyooka et N. Isaka, *V. powersii* (W. Shaw) Printz and *V. spermatosphaera* Powers) or heterothallic, with separate male and female clones (as a result, sexual reproduction

cannot occur within the clonal population) (*V. gigas* Pocock). There are also species with disjunct distribution: for example, heterothallic *V. rousseletii* G. S. West — Africa and Japan (Kimbara *et al.*, 2019) and homothallic *V. capensis* M. F. Rich et Pocock — South Africa and the USA (Nozaki *et al.*, 2015b).

An attempt was made to trace a correlation between the latitudinal distributions of *Volvox* species and the type of light-dark control during asexual life cycles (Desnitskiy, 2016). In this regard, the diversity of gonidial division patterns within the genus *Volvox* is noteworthy (Desnitski, 1992, 1995; Herron *et al.*, 2010). In a number of species (e. g., *V. africanus* G. S. West, *V. carteri* F. Stein, *V. powersii* and *V. spermatosphaera*), the asexual development cycle is characterized by a fast and light-independent series of consecutive divisions of gonidia (asexual reproductive cells). The interval between two divisions is no more than 1 hour. Such a developmental cycle is called palintomic. By contrast, in other species (*V. aureus*, *V. barberi* W. Shaw, *V. globator*, *V. rousseletii* and *V. tertius*) there is a reduced form of palintomy during asexual reproduction: gonidial divisions are light-dependent and slow (the interval between two consecutive divisions lasts 3 or 4 h). It should be noted that the process of gonidial growth is light-dependent in all *Volvox* species (Kirk, 1997). However, *Volvox* is the only genus of colonial Volvocales, within which there are species with both palintomic and non-palintomic cycle of asexual development; in other colonial volvocine genera, all species are characterized by the palintomic cycle of asexual development (Coleman, 2012). The phylogenetic analysis (Herron *et al.*, 2010) shows that the reduction of palintomy (the transition from the palintomic pattern of asexual life cycle to the nonpalintomic one) is a derived event and had independently occurred in three evolutionary lineages of *Volvox*.

The family Volvocaceae, for which there are no reliable fossil records, originated, according to a multigene data set (Herron *et al.*, 2009), at least 180 million years ago (MYA). The use of literature data on paleoclimatology (Pross *et al.*, 2012) and continental drift in the geological past of the Earth (Scotese, 2001), gave reason to assume that the differences in light/dark control and rate of reproductive cell division among *Volvox* species evolved as a result of latitudinal differences in day length during early Cenozoic (probably in Paleocene or early Eocene warm epochs), when suitable *Volvox* habitat existed in high northern and southern paleolatitudes. A detailed consideration of such a hypothesis on *Volvox* evolution (Desnitskiy, 2016), however, is not within the scope of this article.

Returning to the extant *Volvox* species, it is appropriate to note that the analysis of their geography (Desnitskiy, 2016) clearly shows 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 and light-dependent cell divisions start in the morning and the process of gonidial 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. On the other hand, in the

Southern Hemisphere southward of 35–36°S, only five species with slow and light-dependent gonidial divisions occur: *V. aureus*, *V. barberi*, *V. globator*, *V. perglobator* Powers, and *V. tertius* (Chapman *et al.*, 1957; Parra *et al.*, 1983). Interestingly, the palintomic *Volvox* species (rapid and light-independent cleavage) and species with reduced palintomy (slow and light-dependent cleavage) successfully coexist in the lower latitudes of both hemispheres (between 52–57°N and 35–36°S) (Iyengar, Desikachary, 1981; Ettl, 1983).

It is worth pointing out that waterfowl can play a role in the dissemination of thick-walled and dormant zygotes of volvocine algae (Coleman, 1996, 2012). The general theme of the waterbird-mediated dispersal of aquatic organisms is well known in modern ecology (Santamaria, Klaassen, 2002). This fact deserves attention when discussing the geography of extant Volvocales. However, bird migrations over long distances most likely arose in the middle Eocene (i. e., probably around 45 MYA) (Louchart, 2008). Therefore, it is reasonable to admit that in the absence of migratory birds, the early Cenozoic flora of colonial volvocine algae included only very few species (if any) with a wide distribution (simultaneously on several continents).

Problem of species structure and its impact on the biogeography of colonial Volvocales

About 60 years ago, the first studies of species structure were performed on two cosmopolitan representatives of the family Volvocaceae: *Pandorina morum* (Coleman, 1959) and *Eudorina elegans* (Goldstein, 1964). The authors demonstrated the phenomenon of sexual isolation between natural populations of morphologically identical (at the light microscopic level) individuals of the same species. It should be noted that these studies were conducted under the guidance of eminent phycologist Richard Starr. In subsequent years, the problem of the species structure was most intensively analyzed in *P. morum* by Annette Coleman. It turned out that this morphologically uniform species actually consists of numerous (more than 25) reproductively isolated mating groups (syngens). Interestingly, sometimes two syngens can be found in the same pond. Earlier studies (Coleman, 1977; Coleman, Zollner, 1977) focused on the phenomenon of sexual isolation, as well as variations in haploid chromosome numbers (from 2 to 14) and zygote arrangement patterns (clumped or scattered). More recent studies (Coleman *et al.*, 1994; Schagerl *et al.*, 1999; Coleman, 2001, 2009) focused on molecular and biochemical traits (including ITS-2 sequences). Most *P. morum* syngens are locally distributed (within a few dozen of kilometers or even within one small body of water), but a few others are very widespread and it cannot be excluded that they are cosmopolitan. For example, heterothallic syngen II was found in the USA (California, Indiana, Iowa, Texas), Nepal, and Thailand, whereas heterothallic syngen XX is known from the USA (Massachusetts), China, India, Japan, and South Korea.

Molecular and biochemical studies on *Eudorina* (Angeler *et al.*, 1999; Coleman, 2002) supported previous results (Goldstein, 1964) about occurrence of several syngens in *E. elegans*, but simultaneously noted an unsatisfactory state in the taxonomy

of this genus. Precise delimitation of species of *Eudorina* was problematic due to a paucity of data (Nozaki *et al.*, 1997; Angeler *et al.*, 1999).

It was originally believed (Coleman *et al.*, 1994) that the cosmopolitan alga *Gonium pectorale* has only one syngen (no reproductive isolation between individual populations) and so its species structure might be different from that of *Pandorina morum* or *Eudorina elegans*. However, more recent studies (Fabry *et al.*, 1999) based on molecular and breeding analyses of 25 isolates from five continents showed that *G. pectorale* consists of two syngens. The first syngen was found in Europe, Asia, North America and South America, while the second syngen was revealed only in South Africa and South America. It is appropriate to remark that data on *G. pectorale* from the sixth continent, Australia, were not included because the Australian isolate of this alga was lost before the research was completed. Taken together, the molecular and genetic studies of the species structure in the representatives of *Pandorina*, *Eudorina* and *Gonium* suggest the presence of cryptic taxa among colonial Volvocales. On the other hand, the molecular analysis of *Yamagishiella unicocca* (Rayburn et R. C. Starr) Nozaki (15 isolates from Europe, Asia, North America and South America) showed that it is a genetically uniform taxonomic species, despite some variations in colonial vegetative morphology (Coleman, 2001). Therefore, this work supports the idea about a single syngen in the monotypic genus *Yamagishiella* Nozaki.

It is appropriate to remark that the first works on species structure and reproductive isolation in the colonial volvocine algae (Coleman, 1959; Goldstein, 1964) followed the pioneering studies on syngens in ciliates (Sonneborn, 1957). Later, former 14 syngens of *Paramecium aurelia* Ehrenb. were recognized as 14 sibling species, each with a new Latin name (Sonneborn, 1975). On the other hand, there is some ambiguity regarding the rank of syngens of *Pandorina morum*, *Eudorina elegans* and *Gonium pectorale* as new biological species, since the corresponding taxonomic work has not yet been carried out.

Finally, the situation with the problem of infraspecific taxonomy of *Volvox* should be considered. There are several infraspecific taxa of *V. carteri*, the most studied member of the genus (Starr, 1971a; Nozaki, 1988). In culture, sometimes the sexual pheromone of one form of *V. carteri* can stimulate sexual differentiation in another form of the same species (Nozaki, 1988; Kirk, 1997). However, intercrossing data are more important. Two Japanese heterothallic strains, *V. carteri* f. *kawasakensis* Nozaki and *V. carteri* f. *nagariensis* M. O. P. Iyengar, exhibited the unilateral production of mature hybrid zygotes only after mixing the female strain of *V. carteri* f. *kawasakensis* and the male strain of *V. carteri* f. *nagariensis*. The progeny was not viable, though, indicating a genetic barrier between the two forms (Nozaki, 1988). *Volvox carteri* f. *nagariensis* and *V. carteri* f. *weismannia* (Powers) M. O. P. Iyengar are also not interfertile (Kirk, Harper, 1986). Therefore, in principle the forms of *V. carteri* might be regarded as separate species. On the other hand, within the taxon *V. carteri* f. *nagariensis*, a significant trend towards genetic isolation is incomplete, since the geographically isolated Japanese and Indian strains of this form are in-

terfertile. Despite the high lethality rate (up to 93–94%), viable progeny can be obtained (Kirk, Harper, 1986; Adams *et al.*, 1990).

Remarkably that in the classical monograph of the genus *Volvox* (Smith 1944), heterothallism or homothallism were considered to be among important characteristics for the delimitation of species. To continue addressing the problem of species structure in *Volvox*, let us turn to works on the features of sexual reproduction in *V. africanus* (Starr, 1971b) and *V. dissipatrix* (W. Shaw) Printz (Starr, 1972). In the first paper, Starr reported four types of sexuality (including both heterothallism and homothallism) in several strains from four continents identified as *V. africanus*. He concluded the article (Starr, 1971b: 66) with the following words: “I do not propose at this time to establish new species to include the several sexual types. Further study is needed of the time and control of differentiation in the various types, and attempts must be continued to intercross the different strains. Until such information is at hand it would not contribute to any clarification of the genus by adding new specific epithets”. It was reported in a subsequent short publication (Starr, 1972) that another species, *V. dissipatrix*, also includes both heterothallic and homothallic strains.

More than forty years passed since then, and the revisions of these species were made using new molecular, genetic and morphological data. At first, *Volvox africanus* was delimited into two closely related species, homothallic *V. africanus* and heterothallic *V. reticuliferus* Nozaki (Nozaki *et al.*, 2015a). Secondly, *V. dissipatrix* was delimited into homothallic *V. dissipatrix* and heterothallic *V. zeikusii* Nozaki (Nozaki *et al.*, 2019b). On the other hand, sometimes molecular data suggest that two closely related lineages may represent a single *Volvox* species with extensive morphological diversity, as appears to be the case in *V. ferrisii* (Nozaki *et al.*, 2016). It should be noted that occasionally a description of a new species (via species delimitation) can cause certain problems with respect to the data on *Volvox* distribution. For instance, *V. africanus* is known today from Japan, India, Philippines, Africa, and the USA, while *V. reticuliferus* from Japan and Australia (Nozaki *et al.*, 2015a). Therefore, some earlier records of “*V. africanus*” in South America (Parra *et al.*, 1983) cannot be used now for a review of either *V. africanus* or *V. reticuliferus* distribution.

In this regard, a few words should also be said about homothallic *Volvox aureus* (the only cosmopolitan member of the genus). This species is represented not only by strains with sexual reproduction and zygospore formation (Darden, 1966), but also by strains, in which male colonies are absent or extremely rare (Darden, 1968; Starr, Zeikus, 1993; Desnitski, 2000). In old cultures of such strains, many gonidia are transformed into parthenospores, which were presumed to be haploid (no cytological or genetic analysis was performed), though they have the same appearance as mature diploid zygotes. These data support the idea of the ecological and morphological diversity of *V. aureus*. On the other hand, representations of the world-wide distribution of this species are based on the numerous records that were collected for over a century. But what would happen, one may ask, if *V. aureus* is delimited into two species? The consequences might be greater than in the case of *V. africanus* delimitation discussed above.

We would not be able to use the vast majority of the earlier records of “*V. aureus*”, based on the morphology of vegetative (asexual) colonies, to review the geography of *V. aureus* sensu stricto and a new *Volvox* species.

In conclusion, it is appropriate to remark that recent advances in the descriptions of new cryptic taxa of the colonial Volvocales have significantly complicated the work of field biologists making checklists of freshwater algae around the world. In the same time, a handful of qualified experts in the taxonomy of colonial volvocine algae (conducting complex molecular and morphological analyses in culture) will hardly be able to process the huge data on the global distribution of this group. Thus, at present, it is easier to explain some particular patterns, such as the peculiarities of latitudinal distribution of the genus *Volvox*, than to compile a comprehensive review on the geography of all species of the family Volvocaceae. Let us remind that not only Herron and Nedelcu (2015), but also Nanjundiah *et al.* (2018) pointed to the sad state of the species problem and taxonomy of the colonial volvocaceans, referring primarily to the example of “*Pandorina morum*”. However, similar difficulties in describing new cryptic taxa also arise in studies of many other groups of algae (e. g., De Clerck *et al.*, 2013; Leliaert, De Clerck, 2017). This fact, obviously, reflects one of the trends in modern phycology.

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