

On the origins and early evolution of multicellularity

A.G. Desnitski

Biological Institute of St. Petersburg State University, Oranienbaumskoye sch. 2, Stary Peterhof, St. Petersburg, 198904 (Russia)

(Received May 12th, 1992)

(Revision received December 3rd, 1992)

In this paper an attempt is made to consider the significance of recent data on the organization and development of *Volvox*, a multicellular spheroidal green alga, for the unsolved problem of metazoan origins. A brief analysis is made of differences and similarities in some trends and principles during the establishment of metazoan and volvoclean multicellularity.

Key words: Origin of multicellularity; *Volvox*; Lower metazoa; Cell differentiation; Protistan evolution

Transitions from unicellularity to multicellularity occurred many times in the course of eukaryotic evolution. Some tendencies towards achievement of multicellularity can be seen in various lower eukaryotes: flagellates, infusoria, cnidosporidia, algae, cellular slime moulds, etc. (Bonner, 1974; Taylor, 1978; Gilbert, 1991).

Interesting results have been obtained recently in attempts to elucidate the genetic basis for the origin of multicellularity in *Volvox* (Kirk and Harper, 1986; Kirk, 1988; Kirk et al., 1991; Tam and Kirk, 1991). It has been supposed that the appearance of three loci (*regA*, *gls* and *lag*) in the volvoclean genome might have been a prerequisite for the evolutionary transition from a unicellular or colonial state (in which all cells are similar) to the truly multicellular state with a complete division of labour between two fully differentiated cell types. Moreover, some success has been achieved in elucidating cellular mechanisms underlying the evolution of asexual ontogenesis in *Volvox* (Desnitski, 1991, 1992). The *Volvox aureus* type of development, with slow divisions of small gonidia (asexual reproductive cells), seems to be more advanced

in the evolutionary respect than the *V. carteri* type of development, with rapid divisions of large gonidia.

The above studies have stimulated me to consider whether recent data concerning *Volvox* have any significance for the analysis of the problem of metazoan origins, as elaborated during recent decades by many authors (Ivanov, 1968, 1973; Salvini-Plawen, 1978; Grell, 1979, 1981; Corliss, 1989, et al.). On the whole, the latter problem is still quite far from being solved. It is reasonable to consider here mainly those models (e.g. Ivanov, 1968; Salvini-Plawen, 1978) according to which the hypothetical primary metazoons were (like the extant *Volvox*) free-swimming, spheroidal organisms consisting of two basic cell types. In doing so, I should first like to pinpoint the principal differences involved in establishment of volvoclean and metazoan multicellularities, but without giving undue attention to the well-known fact that cells in the body of lower Metazoa are diploid, whereas the cells of a *Volvox* spheroid are haploid.

Because *Volvox* is a phototrophic organism, it is in no need of a special cellular type responsible for nutrition. Thus in this case one sees differentiation into somatic cells (executing locomotory functions) and reproductive cells (executing asexual or sexual reproduction). The

Correspondence to: A.G. Desnitski, Biological Institute of St. Petersburg State University, Oranienbaumskoye sch. 2, Stary Peterhof, St. Petersburg, 198904, Russia.

cells of both types have chloroplasts and carry out photosynthesis, though they differ sharply in the sets of their transcripts and proteins (reviews: Kirk and Harper, 1986; Desnitski, 1991; Tam and Kirk, 1991). It is appropriate to note that the somatic cells of *Volvox*, besides executing the functions that were mentioned above, synthesize the bulk of the extracellular glycoproteinaceous matrix that maintains the organization of the spheroid. In *V. carteri f. nagariensis*, somatic cells were also shown to participate in the response to the sex-inducing pheromone (Jaenicke and Gilles, 1985; Wenzl and Sumper, 1986).

On the other hand, it is quite possible that differentiation of so-called 'kinoblast', the layer of cells with a locomotory function, and so-called 'phagocytoblast', the layer of cells executing a nutritive function, played a leading role during the evolutionary origins of Metazoa (Ivanov, 1968; Salvini-Plawen, 1978). Certainly it is reasonable to suppose that the locomotory and nutritive cells might both execute certain other functions as well (undoubtedly different from the additional functions of the two cellular types in *Volvox*).

Sexual differentiation in the hypothetical primary Metazoa has never been studied in detail, though the zoological works quoted above have supposed that the acquisition of sexual reproduction occurred at certain early stages of metazoan evolution. In any case, one can see here a significant difference from several species of *Volvox* that have differentiated asexual and sexual individuals. (*V. carteri* is a typical example.) Finally it must be stressed that in *Volvox*, unlike the multicellular animals (Monroy et al., 1983), meiosis is not a part of the differentiation programme of the reproductive cells (neither asexual nor sexual ones). Therefore, the vast data on sexual differentiation in *Volvox* and its relatives (reviews: Kochert, 1982; Jaenicke and Gilles, 1985; Kirk and Harper, 1986) can hardly be used productively for the creation of new hypotheses regarding the evolutionary origin of metazoan sexual differentiation.

There is another possible difference between the organization of *Volvox* and that of the pri-

mary Metazoa. In a *Volvox* spheroid, both cellular types occupy strictly fixed positions, whereas a hypothetical 'phagocytella' (Ivanov, 1968) would presumably be characterized by considerable motility of individual cells within the organism. Thus, it is reasonable to suppose that in the course of the establishment of metazoan multicellularity (unlike the establishment of volvoclean multicellularity) the development of selective adhesion of cells had an important role to play.

In *Volvox*, an organism with irreversibly determined somatic cells, there is, beyond doubt, much more profound stability of cellular differentiation than in some extant lower Metazoa. In Cnidaria, for instance, cells of certain types retain the ability to undergo a range of specific transformations. (I will not consider here more advanced invertebrates, such as Ctenophora, Turbellaria, or Nematodes.) In *Hydra* the reproductive cells, as well as a number of differentiated somatic cell types, arise from the interstitial stem cells (Bode and David, 1978; Monroy et al., 1983). In the anthomedusa *Podocoryne carnea*, striated muscle cells are able to transdifferentiate into a number of other cellular types (Schmid et al., 1982). I think that a high stability of the differentiated state (and thus almost total lack of plasticity) in *Volvox*, an extremely primitive multicellular organism consisting of two cell types only, might explain the arrest of the evolution of multicellularity at rather early stages (without forming further cell types). It is appropriate to note that various mutations that change cell differentiation in *V. carteri f. nagariensis* (e.g., $regA^-$, lag^- , or gls^-) do not complicate spheroid organization by increasing the number of cell types. On the contrary, a $regA^-/gls^-$ double mutant results in the formation of a more primitive organism (with only one cell type) resembling *Eudorina* (Kirk et al., 1991; Tam and Kirk, 1991).

Let me now direct attention to the search for similar trends or principles between the establishment of volvoclean and metazoan multicellularity. In both processes an augmentation of cell numbers occurred. This is a good example of 'polymerization', a well-known

principle of protist evolution (Dogiel, 1929). In this connection it is appropriate to recall another well-known principle (this from the field of developmental biology) regarding the minimal critical cellular mass required for subsequent differentiation (e.g. Deuchar, 1970). It is clear that in both cases (volvoclean and metazoan multicellularity) the achievement of a certain minimal number of members in colonies of initially identical cells was a necessary precondition for differentiation into two cellular types.

Recent data on ribosomal RNA sequence analysis in volvoclean flagellates (Larson et al., 1992) have confirmed earlier ideas (Fritsch, 1929; Hoops, 1984) about polyphyletic origins of the genus *Volvox*, though the whole family of the green colonial Volvocaceae (including the genera *Pleodorina*, *Eudorina*, *Pandorina*, *Goniun*, *Platydorina*, *Volvulina*, etc.) represents a monophyletic group, the evolutionary trends within which are more complicated than once imagined and far from being fully elucidated. It should be noted, however, that the aforementioned data on ribosomal RNA sequence indicate that *V. aureus* and *V. carteri* are in the same phylogenetic branch. Nevertheless, these two species (the most thoroughly studied representatives of the genus) differ significantly in certain aspects of morphology and development (Starr, 1970; Kochert, 1975; Desnitski, 1992). Therefore, one can see a possibility for significant diversification of structure and pathways of differentiation, even within a small taxonomic group of primitive organisms consisting of only two cell types. However, it is not clear whether this principle is valid for the hypothetical primary Metazoa.

If it is applicable in the latter case, then there would be some reasons to believe that in the course of metazoan evolution the earliest transition to true multicellularity, with the first division of labour, also occurred within a taxon of a relatively small status: an order or a family. It must be noted, though, that the available palaeontological data concerning the Precambrian fauna (Fedonkin, 1987) suggest extremely low taxonomic diversity of the primary Metazoa at the level of species and, conversely, con-

siderable diversity at the level of the highest taxa. In this connection it is appropriate to emphasize that the taxonomy of the primitive fossil Metazoa, the organisms with several types of somatic cells, is based on quite different morphological criteria than the taxonomy of the extant volvoclean flagellates, which are able to evolve only one type of somatic cells. Taking into consideration the possibility of multiple transitions to multicellularity within a small taxonomic group, as Larson et al. (1992) have suggested recently for the volvoclean flagellates, it would be of interest to consider in the future the question of the taxonomic status of the hypothetical primary metazoons.

On the other hand, bearing in mind the protistan ancestry of the multicellular animals, it would be highly tempting to apply ideas from contemporary evolutionary protistology regarding r- and K-selections (Cavalier-Smith, 1980) to the problem of the origin of the Metazoa. For this purpose, however, one would require a vast amount of information concerning the ancient ecosystems in which the primary Metazoa originated and evolved, information that is not currently available.

References

- Bode, H.R. and David, C.N., 1978, Regulation of a multipotent stem cell, the interstitial cell of Hydra. *Progr. Biophys. Mol. Biol.* 33, 189–206.
- Bonner, J.T., 1974, *On development: the biology of form* (Harvard University Press, Cambridge).
- Cavalier-Smith, T., 1980, r- and K-tactics in the evolution of protist developmental systems: cell and genome size, phenotype diversifying selection, and cell cycle patterns. *BioSystems* 12, 43–59.
- Corliss, J.O., 1989, Protistan diversity and origins of multicellular/multitissued organisms. *Boll. Zool.* 56, 227–234.
- Desnitski, A.G., 1991, Mechanisms and evolutionary aspects of ontogeny of the genus *Volvox* (Chlorophyta, Volvocales) (in Russian). *Bot. Zh. (Leningrad)* 76, 657–668.
- Desnitski, A.G., 1992, Cellular mechanisms of the evolution of ontogenesis in *Volvox*. *Arch. Protistenkd.* 141, 171–178.
- Deuchar, E.M., 1970, Effect of cell number on the type and stability of differentiation in amphibian ectoderm. *Exp. Cell Res.* 59, 341–343.

- Dogiel, V., 1929, Polymerisation als ein Prinzip der progressiven Entwicklung bei Protozoen. *Biol. Zbl.* 49, 451–469.
- Fedonkin, M.A., 1987, Skeletonless Vend fauna and its place in the evolution of Metazoa (in Russian) (Nauka, Moscow).
- Fritsch, F.E., 1929, Evolutionary sequence and affinities among Protophyta. *Biol. Rev. Cambridge Phil. Soc.* 4, 103–151.
- Gilbert, S.F., 1991, *Developmental biology* (3rd edn.) (Sinauer Associates, Sunderland, Mass.).
- Grell, K.G., 1979, Die Gastraea-Theorie. *Med. Histor. J.* 14, 275–291.
- Grell, K.G., 1981, *Trichoplax adhaerens* and the origin of Metazoa. *Atti dei Convegni Lincei* 49, 107–121.
- Hoops, H.J., 1984, Somatic cell flagellar apparatuses in two species of *Volvox* (Chlorophyceae). *J. Phycol.* 20, 20–27.
- Ivanov, A.V., 1968, The origin of the multicellular animals (in Russian) (Nauka, Leningrad).
- Ivanov, A.V., 1973, *Trichoplax adhaerens*: a phagocytella-like animal (in Russian). *Zool. Zh. (Moscow)* 52, 1117–1131.
- Jaenicke, L. and Gilles, R., 1985, Germ-cell differentiation in *Volvox carteri*. *Differentiation* 29, 199–206.
- Kirk, D.L., 1988, The ontogeny and phylogeny of cellular differentiation in *Volvox*. *Trends Genet.* 4, 32–36.
- Kirk, D.L. and Harper, J.F., 1986, Genetic, biochemical and molecular approaches to *Volvox* development and evolution. *Int. Rev. Cytol.* 99, 217–293.
- Kirk, D.L., Kirk, M.M., Stamer, K.A. and Larson, A., 1991, The genetic basis for the evolution of multicellularity and cellular differentiation in the volvocine green algae, in: *The Unity of Evolutionary Biology: Proceedings of the IV International Congress of Systematic and Evolutionary Biologists*, E.C. Dudley (ed.) (Dioscorides Press, Portland, Oregon) pp. 568–581.
- Kochert, G., 1975, Developmental mechanisms in *Volvox* reproduction, in: *The Developmental Biology of Reproduction*, C.L. Markert and J. Papaconstantinou (eds.) (Academic Press, New York) pp. 55–90.
- Kochert, G., 1982, Sexual processes in the Volvocales, in: *Progress in Phycological Research*, Vol. 1, F.E. Round and D.J. Chapman (eds.) (Elsevier Biomedical Press, Amsterdam, New York, Oxford) pp. 235–256.
- Larson, A., Kirk, M.M. and Kirk, D.L., 1992, Molecular phylogeny of the volvocine flagellates. *Mol. Biol. Evol.* 9, 85–105.
- Monroy, A., Parisi, E. and Rosati, F., 1983, On the segregation of the germ and somatic cell lines in the embryo. *Differentiation* 23, 179–183.
- Salvini-Plawen, L.V., 1978, On the origin and evolution of the lower Metazoa. *Z. Zool. Syst. Evol.-forsch.* 16, 40–88.
- Schmid, V., Wydler, M. and Adler, H., 1982, Transdifferentiation and regeneration in vitro. *Dev. Biol.* 92, 476–488.
- Starr, R.C., 1970, Control of differentiation in *Volvox*. *Dev. Biol.*, Suppl. 4, 59–100.
- Tam, L.-W. and Kirk, D.L., 1991, The program for cellular differentiation in *Volvox carteri* as revealed by molecular analysis of development in a gonidialess/somatic regenerator mutant. *Development* 112, 571–580.
- Taylor, F.J.R., 1978, Problems in the development of an explicit hypothetical phylogeny of the lower eukaryotes. *BioSystems* 10, 67–89.
- Wenzl, S. and Sumper, M., 1986, Early event of sexual induction in *Volvox*: chemical modification of the extracellular matrix. *Dev. Biol.* 115, 119–128.