НАУЧНЫЕ ДИСКУССИИ

УДК 591.4+576.3

© 1995 г. A.G. DESNITSKI

ON THE ORIGIN OF METAZOA

Under consideration is a new version of the phagocytella conception. It is suggested to consider blastea not a particular organism but a morphologically variable taxon of mixotrophic flagellates. Some of its subtaxa might have made a transition to the true heterotrophy, thus having become direct metazoan ancestors.

The problem of the metazoan origin is still far from being solved, though important new palaeontological data concerning the Precambrian fauna (Fedonkin, 1987; Conway Morris, 1993) and new molecular data involving comparisons of ribosomal RNA sequences among various unicellular and multicellular organisms (Field et al., 1988; Lake, 1990; Christen et al., 1991; Wainright et al., 1993) have been obtained recently. The studies of molecular phylogeny are contradictory: some authors (Lake, 1990; Wainright et al., 1993) favour monophyletic origin of the Metazoa, while the others (Field et al., 1988; Christen et al., 1991) favour polyphyletic origins.

This note is devoted to a further elaboration of Metschnikoff's (1886) theory of phagocytella (parenchymella) that has obtained further support by later investigators (e.g., Hyman, 1942; Ivanov, 1968; Salvini-Plawen, 1978). According to it, the hypothetical blastula-like flagellate ancestor (blastaea) became two-layered by multipolar ingression of phagocytizing cells. It should be noted that Ivanov (1968) and Salvini-Plawen (1978) favoured colourless colonial flagellates (presumably choanoflagellates) as metazoan ancestors. Such proposition denies Hyman's ideas about metazoan origin from "coloured holophytic flagellates by way of colony formation followed by loss of chlorophyll and assumption of holozoic habits" (Hyman, 1942, p. 30). More recently, however, an idea of the metazoan origin from photosynthesizing flagellates has gained some renewed support (e.g., Taylor, 1978). Moreover, we are now well aware of extensive capacity for both phagotrophy and mixotrophy in various species of phytoflagellates (Porter, 1988; Sanders, Porter, 1988).

In considering the problem of metazoan origins, two principles regarding the evolution of multicellularity obtained from studies of *Volvox* and its relatives seem to be relevant. 1. Significant diversity of structure and pathways of differentiation may exist even within a small taxonomic group of primitive organisms consisting of only two main cell types, i.e. the genus *Volvox* (Desnitski, 1992, 1993; Ransick, 1993; Kirk, 1994). 2. Multiple independent (and reversible) transitions to true multicellular state with a "division of labour" between two cell types may have occurred within a small taxonomic group, i.e. the family Volvocaceae (Larson et al., 1992; Schmitt et al., 1992).

Bearing in mind these principles, it seems reasonable for the present to refrain from trying

to provide a concrete morphological description of "the" blastaea, and to regard it instead as a hypothetical, morphologically variable, lower rank taxon. Some of these phytoplankters, initially mixotrophic, might have made a transition to greater reliance on heterotrophy. Such a change in nutritional mode might offer them an opportunity to occupy new adaptive zones and, in particular, to penetrate into the oligophotic zone of the aquatic ecosystem (depths of more than 50–100 m). Such loss of dependence on photosynthesis might well be expected to be combined with a specific differentiation into two main types of cells, locomotory and nutritive ones, with the latter assuming an internal position within the actively swimming phagocytella. Again, it is probably wise to refrain from trying to give a more concrete morphological description.

It should be stressed that this type of simple transition toward heterotrophy might have been repeated independently in several taxa. So there might have been a number of phagocytella species (with some variations in morphology) existing simultaneously, at least some of which might have represented different steps of early metazoan evolution.

This approach, based on considering primary metazoons as consisting of a number of distinct taxa, makes it possible to circumvent certain difficulties in reconstructing these hypothetical organisms.

REFERENCES

Christen R., Ratto A., Baroin A., Perasso R., Grell K.G., Adoutte A. Origin of metazoans. A phylogeny deduced from sequences of the 28S ribosomal RNA // Ed. Simonetta A.M., Conway Morris S. The early evolution of Metazoa and the significance of problematic taxa. Cambridge: Cambridge Univ. Press, 1991. P. 1–9.

Conway Morris S. The fossil record and the early evolution of the Metazoa // Nature. 1993. V. 361. P. 219–225.

Desnitski A.G. Cellular mechanisms of the evolution of ontogenesis in *Volvox* // Arch. Protistenkd. 1992. V. 141. P. 171–178.

Desnitski A.G. On the origins and early evolution of multicellularity // BioSystems. 1993. V. 29. P. 129–132.

Fedonkin M.A. The Vendian non-skeletonized fauna and its place in the evolution of Metazoa. M.: Nauka, 1987. 176 p. (In Russian).

Field K.G., Olsen G.J., Lane D.J., Giovannoni S.J., Ghiselin M.T., Raff E.C., Pace N.R., Raff R.A. Molecular phylogeny of the animal kingdom // Science. 1988. V. 239. P. 748–753.

Hyman L.H. The transition from the unicellular to the multicellular individual // Biol. Symposia. 1942. V. 8. P. 27–42.

Ivanov A.V. The origin of the multicellular animals. L.: Nauka, 1968. 287 p. (In Russian).

Kirk D.L. Germ cell specification in *Volvox carteri* // Ed. Marsh J., Goode J. Germline development. Chichester: John Wiley and Sons, 1994. P. 2–30.

Lake J.A. Origin of the Metazoa // Proc. Nat. Acad. Sci. U.S.A. 1990. V. 87. P. 763–766.

Larson A., Kirk M.M., Kirk D.L. Molecular phylogeny of the volvocine flagellates // Mol. Biol. Evol. 1992. V. 9. P. 85–105.

Metschnikoff E. Embryologische Studien an Medusen. Wien: Alfred Holder, 1886. 159 S.

Porter K.G. Phagotrophic phytoflagellates in microbial food webs // Hydrobiologia. 1988. V. 159. P. 89–97.

Ransick A. Specification of reproductive cells in *Volvox* // Ed. Spradling A. Evolutionary conservations of developmental mechanisms. N.Y.: Wiley – Liss, Inc., 1993. P. 55–70.

Salvini-Plawen L. On the origin and evolution of the lower Metazoa // Z. zool. Syst. Evol. – forsch. 1978. V. 16. P. 40–88.

Sanders R.W., Porter K.G. Phagotrophic phytoflagellates // Adv. Microb. Ecol. 1988. V. 10. P. 167–192.

Schmitt R., Fabry S., Kirk D.L. In search of molecular origins of cellular differentiation in *Volvox* and its relatives // Int. Rev. Cytol. 1992. V. 139. P. 189–265.

Taylor F.J.R. Problems in the development of an explicit hypothetical phylogeny of the lower eukaryotes // BioSystems. 1978. V. 10. P. 67–89.

Wainright P.O., Hinkle G., Sogin M.L., Stickel S.K. Monophyletic origins of the Metazoa: an evolutionary link with fungi // Science. 1993. V. 260. P. 340–342.

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

Received
15.XI.1995

А.Г. ДЕСНИЦКИЙ

К ПРОБЛЕМЕ ПРОИСХОЖДЕНИЯ METAZOA

Биологический институт Санкт-Петербургского государственного университета, Ораниенбаумское шоссе, 2, Старый Петергоф, 198904, Санкт-Петербург

Предлагается новый вариант теории фагоцителлы – происхождение многоклеточных животных (Metazoa) от планктонных шаровидных колоний миксотрофных фитофлагеллят. Переход некоторых популяций этих организмов к гетеротрофному типу питания предоставил им возможность занять новые адаптивные зоны и, в частности, проникнуть в олигофотическую зону водных экосистем (глубины более 50–100 м). Утрата фотосинтеза коррелировала с возникновением характерной для фагоцителлы дифференциации на кинобласт, наружный пласт клеток с локомоторной функцией, и фагоцитобласт, внутренний пласт клеток, выполняющих функцию питания.