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THE GERM SIMILARITY IN ONTOGENY OF CILIATES (CILIOPHORA)

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The Germ Similarity in Ontogeny of Ciliates (Ciliophora). Dovgal I. V. — The paper deals with the regularities of ontogenesis of mobile and sessile ciliated protozoans. It is shown, that the germ similarity is characteristic both in mobile and sessile ciliates. The mechanisms of controlling of morphogenesis in ciliates are probably homologues with the controllers of early morphogenesis in multicellular organisms. The special statement for the case of law of germ similarity in unicellular eucaryots named "principle of tomits similarity" has been offered.

Key words: ciliates, ontogeny, germ similarity, recapitulation.

Зародышевое сходство в онтогенезе инфузорий (Ciliophora). Довгаль И. В. — В статье рассматриваются особенности онтогенеза подвижных и прикрепленных инфузорий. Показано, что зародышевое сходство проявляется как у подвижных, так и у сидячих форм. Механизмы регуляции онтогенеза у инфузорий и ранних этапов морфогенеза многоклеточных, вероятно, гомологичны. Предложена специальная формулировка закона зародышевого сходства для онтогенеза одноклеточных эукариот — принцип сходства томитов.

Ключевые слова: инфузории, онтогенез, зародышевое сходство, рекапитуляция.

Introduction

The concepts on the modifications during protist life cycle as ontogenesis have developed from the beginning of twentieth century. It should be mentioned that B. P. Tokin (1934) was the pioneer has applied the term "ontogeny" for the protist (ciliate) development. It is known, that the additional information for the reconstruction of protist phylogeny can be obtained through the comparative study of their ontogenesis (Eisler et al., 1995). In this connection it should be noted the peculiarities of the anlage of organelles in protist ontogeny from the point of view of common regularities of individual development.

Although some specialists disclaimed the presence of ontogeny in not colonial protists (Sewertzoff, 1939), the problem of the biogenetic law applicability to protist ontogenesis have been considered in detail in several publications (Hadzi, 1952, Dogiel, 1951, Dogiel et al., 1962, Corliss, 1968, Eisler et al., 1995, Foissner, 1996, etc).

In particular V. A. Dogiel (1951) marked that it is necessary to search the examples of recapitulations in those protists that changed the mode of life during phylogenesis. The most typical case is the transition of protists to the sessile mode of life. As most characteristic example of recapitulation in protist ontogeny the formation of suctorian ciliated tomits have been mentioned. The similar occurrences also were marked in peritrichs. In protists ontogeny there are some examples of the archallaxis, very few cases of the deviation and greater examples of the anaboly.

In the review paper by M. Canella (1964) the study of ontogenesis have been considered as the useful approach in construction of the natural system of infusoria. However this author have considered, that the time history of infusoria ontogenesis may be essentially influenced with ecological and other poorly investigated factors. This makes using of regularities of ciliate individual development for reconstruction of their phylogeny difficult.

It is the A. V. Jankowski's (1972) opinion, that the ontogeny took place in any ciliates and begins from the moment of anlage the fragment of tomit kinetom. The ontogeny finished to the anlage of the similar fragment in a new generated trophont. A. V. Jankowski has recognized the following stages of ontogenesis in ciliates (fig. 1, 2–I): tomit (the bud that separated from parental cell, or the cells are derived as a result of binary fission); trophont (the feeding organism); tomont (the trophont, at which the anlage of tomit ciliature is occurs); protomit (tomit that bounded with parental cell).

Using data on ontogeny, A. V. Jankowski (1972, 1973) have reconstructed the phylogeny of chonotrichs and morphology of a hypothetical ancestor of these ciliates. For this author's opinion, the ontogeneses of chonotrichs, pilisuctorids, hymenostomats, thygmotrichs and rhynchodids are clear examples of anaboly.

Under the J. Corliss' (1968) opinion, the examples of recapitulations of ancestral characters might be found in many taxa of protists. Especially it concerns the groups with complicatedly organized structures such as pellicle or various skeletal structures. The such examples can be detected in mixosporidians (sculpture of spore-valves), gregarine protozoa (diversified gametocyst membranes), coccidians, dinoflagellates (structure of the thecal plates) and other flagellates (mastigont system).

However, the greatest number of similar examples is obtained at study of individual development of ciliates that is connected with high complexity of pattern of their ciliature. As J. Beisson (1994, p. 15) has marked "... ciliates face a true developmental problem: reconstruct the "imago" from part or remnants of its pattern".

The peculiarities of ontogeny usually were applied for establishment of the systematic position of some ciliates taxa (see Eisler et al., 1995). In fact, only applicability of the biogenetic law to protist phylogeny reconstruction have been shown in majority of the above mentioned works.

As for recapitulations, they are analyzed at reconstruction of phylogeny of mobile infusoria, and in such aspect the stomatogenesis (Corliss, 1968; 1979, Foissner, 1996) and reorganisation of cyrries at infusoria (Eigner, 1997) are considered only. The processes of swarmer metamorphosis have employed only at reconstruction of chonotrich ciliates phylogeny (Jankowski, 1973). Finally, W. Foissner (1996) has applied the Hennig's cladistic method to the ontogenetic data of ciliates.

In our opinion the matter what structures are recapitulated in the process of ontogenesis in sessile ciliates is still an open question. The purpose of the present paper is the attempt to estimate which regularities of ontogeny both mobile and sessile ciliates can help to recognize their phylogenetic relationships.

Some regularities of ontogenesis in mobile and sessile ciliates

As indicated above, the recapitulations are usually discussed in the course of stomatogenesis where mobile ciliates concerned.

The first stage of stomatogenesis is neoformations of kinetosomes that compose the anlage of future oral ciliature. This anlage (or anarchic field) variously builds up in different ciliate taxa. The different modes of stomatogenesis are correspondingly distinguished (Foissner, 1996). However, as marked J. Corliss (1968), these modes do not relate directly to large taxa of ciliates. The stomatogenesis is by no reflects the stages of phylogenesis. W. Foissner (1996) has discussed that no stomatogenetic mode can be established for ciliates that lack an oral infraciliature (astomatous ciliates, suctorians, rhynchodids, etc).

In the case of telokinetal stomatogenesis in which formation of the new oral apparatus occurs by involvement of the anterior parts of somatic kineties (Corliss, 1979), it is felt that the oral ciliature was formed by the anaboly. The stages of the such apparatus development in phylogenesis are recapitulated as the result. The same is probably true (with some stipulations) for parakinetal stomatogenesis in which the anarchic field is derived directly from some postoral somatic kineties of parental cell.

However in the case of buccokinetal stomatogenesis in which the new kinetosomes have originate near the organelles of parental buccal apparatus (but not derived from them) and, especially in the case of apokinetal stomatogenesis in which the new oral kinetosomes have no pre-association with parental somatic or buccal kineties we are probably dealing with results of archallaxis. The two last mentioned modes of oral apparatus development accordingly give no way of phylogenetical reconstruction, but testified only that there are possible affinities between taxa with the same mode of stomatogenesis.

Except for stomatogenesis the process of shaping the complex pattern of somatic ciliature in ontogeny also can tell us a lot about ciliate phylogeny. For example, in P. Eigner's (1997) investigation of morphogenetic anlagen developments in the ventral cirral rows in Oxytrichidae is shown, that their very similar pattern originated at least from two different phylogenetic lineages.

During transition of protists to sessiling in connection with the motility loss the problem of expansion appears inevitably. In such case the transition to irregular division with formation of migratory stage saving organelles of locomotion was beneficial. It gave additional benefits since the mother individual did not require transformation. Thus it remained active and reserved the occupied localization that was important in conditions of the topical competition (Dovgal, 2000).

Therefore the evolution of sessile protists life cycle took place at the expense of the adding of new stages (telotrochs, swarmer, etc) (i. e. anaboly after Sewertzoff). In its turn the ontogenesis of sessile protists was reduced to formation and development of these migratory stages. Hence the ontogeny of the sessile ciliates included three stages: formation of the migratory stage, expansion and choice of substrate and metamorphosis of the migratory stage after adhesion.

In majority sessile ciliates either buccokinetal (in peritrichs) and apokinetal stomatogenesis (in chonotrichs) is characteristic. As regards the others morphogenetical processes, they pass is closely resembles in the different groups (Dovgal, 2000). The common scheme of the ontogenesis of sessile ciliates can be considered by the example of chonotrichs (fig. 1).

The life cycle in the chonotrich ciliates begins from the anlage the fragment of tomit ciliature. Next the generated tomit separating and settle to the substrate after short-term swimming. In the course of metamorphosis the swarmer of chonotrich ciliate has gone through the some stages that are similar to the assumed ancestors (fig. 1, 4).

In the peritrichous ciliates the tomit (telotroch) is formed by pseudo-longitudinal (Dogiel, 1951) (or more precisely enantiotropic (Foissner, 1996) binary fission of parental cell. The ontogenesis begins from the doubling of the peristome and the anlage of the locomotor ciliature of telotroch. After the attachment to the substratum by scopula the telotroch loses the locomotor ciliature and the stalk or lorica (if are provided) is secreted.

The budding starts in the suctorians with an invagination of a part of the cell cortex. This parental fragment bearing some basal bodies that later give rise to the cilia of the tomit (swarmer). Apart from kinetosomes the swarmer derived the nuclea and anlagen (axonemes) of tentacles (or completed tentacles) from parental cell. After the settlement the adhesive organelle (i. e. stalk, etc) is formed (Bardele, 1970).

Discussion and conclusions

According to A. N. Sewertzoff (1939) biogenetic law is exhibited only when the sequence of anlage of ancestral characters is recapitulated. As a rule such sequence is exhibited if the evolution of ontogenesis of structures went on by way of anaboly of consequent stages. As shows the literature data, this criterion was not directly applied in the search for the possible recapitulations in ontogenesis of ciliates.

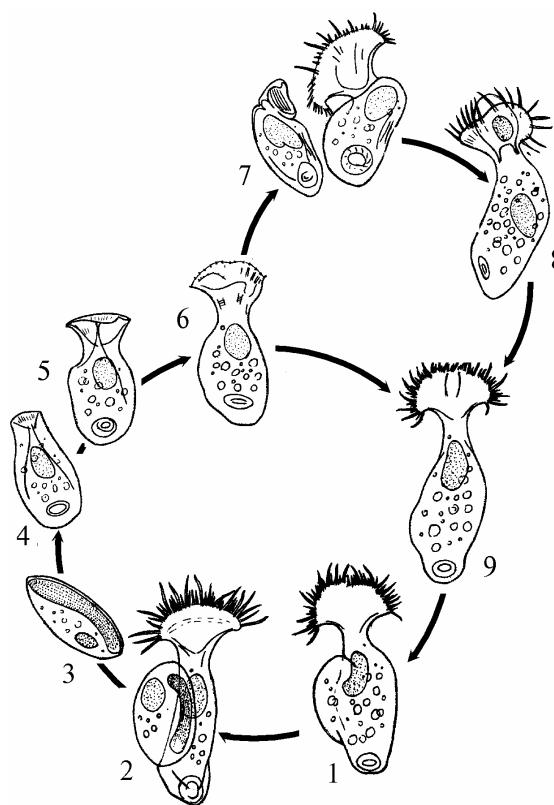


Fig. 1. The life cycle of *Heliochona pontica*: 1–2 — protomit; 3 — tomit; 4 — the stage of phialochona (hypothetical ancestor); 5–6 — metamorphosis of the swarmer; 7–8 — conjugation; 9 — trophont.

Рис. 1. Жизненный цикл *Heliochona pontica*: 1–2 — протомит; 3 — томит; 4 — стадия фиалохоны (гипотетический предок); 5–6 — метаморфоз бродяжки; 7–8 — конъюгация; 9 — трофонт.

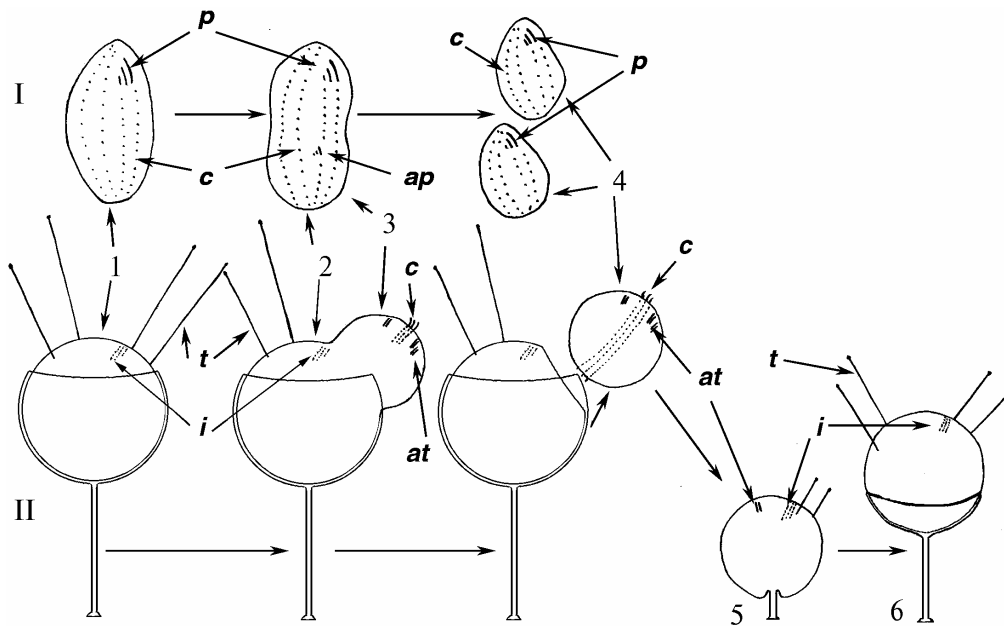


Fig. 2. The ontogeny of mobile (I — after A. V. Jankowski, 1972 with changes) and sessile (II — by the example of suctorians) ciliates (schematic): 1 — trophont; 2 — tomont; 3 — protomit; 4 — tomit; 5–6 — metamorphosis of the tomont; *c* — ciliature; *i* — infraciliature; *at* — anlage of the tentacle; *t* — tentacle; *p* — oral ciliature; *ap* — anlage of the oral ciliature.

Рис. 2. Схема онтогенеза подвижных (I — по А. В. Янковскому, 1972 с изменениями) и сидячих (II — на примере сукторий) инфузорий: 1 — трофонт; 2 — томонт; 3 — протомит; 4 — томит; 5–6 — метаморфоз бродяжки; *c* — цилиатура; *i* — инфрацилиатура; *at* — зачаток шупальца; *t* — шупальце; *p* — ротовая цилиатура; *ap* — зачаток ротовой цилиатуры.

It is necessary to mark that as has been shown by A. N. Sewertzoff (1939) and I. I. Schmalhausen (1969) the recapitulations are not characteristic for early stages of ontogenesis. The archallaxis or deviations in development of structures are much more spreaded.

If the morphogenesis of the mobile ciliates is conceived schematic (fig. 2–I), so it can be seen that overall morphogenesis is actually finished in the stage of protomit. The processes that can be considered as the recapitulations are seen at the same stage.

As with the other protists the ontogenesis of the sessile ciliates begins from the moment of formation of derived cell rudiments, but unlike the mobile forms the derived cell is usually a migratory stage (telotroch, swarmer, etc.). Accordingly, ontogenesis of these protists is prolonged. At the first stage of ontogenesis (fig. 2–II) at migratory stages organelles of locomotion, nuclear apparatus, organelles of a feed and secretion of stalks developed. The derived cells receive the enumerated structures or their rudiments from the parental cells. The second is stage of swimming and selection of substratum. The last stage of ontogenesis is the metamorphosis of a migratory stage after attachment. At this stage usually organelles of locomotion disappear (or they lose the function of locomotion) where the adhesive organelles (in case of chonotrich ciliates also peristomal funnel) are formed.

In sessile ciliates the above mentioned sequence of ancestral characters is not exhibited during forming of tomit. For example, oral structures of the tomits of chonotrichs are considerably simplified in comparison with the homologous structures of their disteriid ancestor's. Tomits of sessile ciliates are more similar with derived individuals of free-swimming infusoria in some sense. The sequence of formation of adhesive organelles, loricas, peristomal funnels, etc at stage of metamorphosis of a swarmer

only can be considered as the recapitulations. But what represents then the text-book examples with swimmers of suctorian and chonotrich ciliates?

In our opinion the emerging of some ancestral characteristics at the early stages of morphogenesis (during formation of tomit) or the stages that are similar to the assumed ancestors (during swimmer metamorphosis in sessile ciliates) are probably manifestations of the law of germ similarity.

If the concept of recapitulation has come into common use by protozoologists, so the germ similarity essentially never discussed. The J. Corliss' (1968) paper is probably unique protozoological work in which along with the recapitulations the law of embryonal similarity ("the fourth law") by K. Baer (1828) also has been mentioned. However the author considers the Baer's law only as extended statement of the Haeckel's et Muller's law.

In difference in the Russian literature (Sewertzoff, 1939; Schmalhausen, 1969; Ivanova-Kazas, 1992; Dondua, 1993) was stated, that the law of embryonal similarity and biogenetic law are provided by different mechanisms. N. Løvtrup (1986) have reached to the same conclusions independently. This author proposed to discriminate between "Baer's recapitulations" (i. e. embryonal similarity) and "terminal recapitulations" (i. e. exhibited by anaboly after A. N. Sewertzoff).

It is necessary to stress that biogenetic law today was not taken seriously by embryologists (Gilbert et al., 1997). While the regularities of morphogenesis which are fall into the law of embryonal similarity recently was supported on the molecular level (Dondua, 1993).

A. N. Sewertzoff (1939) was the pioneer has paid attention to phylogenetical value of K. Baer's law. After A. N. Sewertzoff's opinion, the sequence of characters of adult animal emerging in early ontogenesis corresponds to the sequence of these characters in phylogenesis. In contrast, the biogenetic law shows, in what sequence were anlage the characteristics that existed in ancestors of the animal but than were substituted with other characters. Consequently, in the latter case the characters of adult animal are not recapitulated.

The possible mechanisms of the embryonal similarity were discussed also with invoking of the data on plants development (Schmalhausen, 1969). Probably the Baer's law applies to all cases of ontogenesis, including the individual development of protists (Dovgal, 1999, 2000).

The manifestations of this regularity are connected with the mechanisms of regulation of morphogenesis. The developmental conservatism of early stages of ontogeny promotes preservation (and manifestation) of ancestral characteristics (Schmalhausen, 1969).

At present the regulation of early morphogenesis linked with action of integrated systems of gene interactions (Ivanova-Kazas, 1992, Dondua, 1993). These systems are very conservative and are detected at quite diverged organisms. The homeodomains represent these systems in the insects, vertebrates (Gilbert et al., 1997), plants and yeasts (Kappen et al., 1993; Kappen, 2000; Zraisky, 2001). It is the C. Kappen's (1995) opinion that all eucaryotic organisms derive from ancestors that already possessed a homeodomains early during evolution. For our opinion, the detection of homeodomains in yeasts (Kappen, 1995) testifies that homologues systems of early morphogenesis regulation must exist both in unicellular (include protists) and multicellular eucaryotic organisms. Consequently, the similar regularities must be reflected in their ontogenesis.

External manifestations of the Baer's law in ciliates display certain specificity. In all probability, the structures of cell cortex are of first importance in controlling of morphogenesis.

For example, as the polarity of kineties in ciliate changes with micrurgy, the new pattern is conserved during some following generations of up to conjugation. As J. Beisson (1994) has discussed the cilia and their basal bodies which are anchored in

the cortex are of importance in ciliate morphogenesis (patterning). In our opinion the instance of stomatogenesis is also suggests that the cortical structures has a dominant role in morphogenesis.

Under A. Lwoff's (1990) hypothesis the modifications of the argyrome pattern in suctorian ciliate *Podophrya fixa* (Muller) during budding, which was observed by the author (Lwoff, 1950), is associated with rearranging of cortical proteins. It is the A. Lwoff's (1990) opinion that this rearranging is the case by a Monod-Changeux-Jacob principle. We believed, that the process reflects the function of the cortical structures in controlling of morphogenesis without regard to its possible mechanism.

We can consider that there is good reason to propose the special statement of the regularity of ontogeny in unicellular eucaryots that has been labeled as the principle of tomits similarity. The I. I. Schmalhausen's (1969) definition of the Baer's law was used as a basis for our statement:

1. The tomits display the certain similarity in the limits of phyla of protists at the early stages of morphogenesis.

2. In the course of metamorphosis the tomits sequentially transforms from displaying the common characters of the phylum to manifestation of increasable peculiar characters. The characters which are indicative of the belonging of tomit to the certain genus and species are developed at a later.

3. During metamorphosis the tomits of various representatives of one phylum are more and more diverged.

The mechanisms of controlling of morphogenesis in ciliates (and most likely in all protists) are probably homologues with the controllers of early morphogenesis in multicellular organisms. The specificity of individual development of unicellular eucaryots is in the more essential governing of the cell cortical structures. The similar role in multicellular organisms the cortex probably plays only at stage of the egg ooplasmic segregation (see Kostyuchenko et al., 2000).

Therefore the tomit similarity may occur at the all stages of ciliate ontogeny and gives an information for installation of the taxa relations. The investigation of this regularity is probably the most perspective in solving of phylogenetical problems in ciliates.

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