*Trichoplax adhaeren*s (Placozoa) – The origin of metazoan life?

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Introduction

Regarding evolutionary biology a group of organisms, called a phylogenetic unit, have one common ancestor. For example all humans supposably derived from a common ancestor named Australopithecus afarensis, who lived about three million years ago (Kimbel et al. 1994). Reconstructing this evolutionary young branch of the Tree of Life is comparatively easy, because well-preserved fossils are found. To trace back the basal parts of the Tree of Life is more difficult. Here it is inevitable to use multidisciplinary tools to recreate the evolution of the first metazoan life. There are many hypotheses which claim that recent organisms is most similar to this last common ancestor of all metazoa called the "Urmetazoon" (Schierwater et al. 2009a; Müller et al. 2004). I want to propose a possible candidate for being the most likely Urmetazoon: The hairy plate Trichoplax adhaerens fulfils all requirements for being the mother of all metazoa.

Trichoplax adhaerens is so far the described representative of phylum Placozoa. It is a tiny, marine animal, which usually lives in warm tropical and subtropical oceans distributed up to 50 degrees latitude from the equator. This animal is also found in many warm salt-water aquariums.

The bauplan of Trichoplax adhaerens

The best description of *Trichoplax adhaerens* is the translation of its name: "*hairy plate, which is sticking*". It describes vividly the bauplan and the behaviour of this tiny, marine animal. There is no constant or regular shape and just five somatic cell types, organized in three cell-layers (Schierwater et al. 2005):

The upper epithelium lies on top and is made up of ciliated cells. Irregularly dispersed in this upper epithelium cells are lipid-rich objects, called shiny spheres. The function of this spheres is unknown, it could be a lipid-deposit or it is possibly involved in a anti-predator defense strategy (Jackson et al. 2009).

The lower cell-layer is consisting of two cell types. The first are the gland cells, which excrete digestionenzymes to the bottom-outer space of the animal. The second are the lower-epithelia cells, which are ciliated. They show a compact density outwardly, because the high number of cilia are necessary for sticking to surfaces and locomotion.

The cell-layer which lies in between the two epithelia is the network of fiber cells. This syncyticum of cells is under suspicion to be a very rudimental neuronetwork.

Additionally a fifth cell-type is postulated, which is located at the connecting zone of the two epithelia (Schierwater et al. 2009b).

Reproduction

At first sight Trichoplax looks very simple with its solely five cell types. But there are still hundreds of fundamental questions about this animal, which could not be answered, yet. One of the biggest enigma is their way of sexual reproduction. Sexual interbreeding could not be observed under laboratory conditions, but there are genetic evidences for this (Signorovitch et al. 2005). In addition oocytes and spermcells were observed (Grell et al. 1974; Srivastava et al. 2008). Whereas the development of the zygote never reaches the 512-cell stage under observation in the laboratory (Schierwater 2005). The usual method of reproduction of this animal in laboratory culture is via fission. In the course of this, the two poles of the animal move into different directions until the connection of both breaks apart.

Genome structure

With 98 million basepairs *Trichoplax* possesses the smallest metazoan genome (Srivastava et al. 2008). About 11.500 protein-coding genes are predicted and nearly 14.500 expressed sequence tags (ESTs) are estimated. The intron-structure is comparable to other eumetazoa and higher metazoa. The last point contradicts the hypothesis, that *Trichoplax* could be a reduced Cnidarian, because reduction of organisms comes along with massive intron-loss.

Hox-genes called "Trox" analogue to cnidarian Hoxgenes (Cnox) are found. This kind of genes are involved in determinating body-axis and are also responsible for proper anatomical development. The expression-patterns of Trox are the only known (with the exception of the related gene "Not") of the *Trichoplax* body plan.

Biodiversity

Because of the poor knowledge about sexual reproduction in Trichoplax it is hard to define different species in the phylum of the Placozoa. A common definition of species after Ernst Mayr (de Queiroz 2005) is: "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups". This can not be used for Placozoa yet. In this case a useful tool is genetics. An established gene for comparing different taxa like species is the 16Sribosomal-RNA (Delsuc et al. 2005). Applying this method it could be shown that the diversity inside the Placozoan is greater than expected (Schierwater et al. 2010). The divergence between the 16S-sequence of different Trichoplax specimens is comparable to the divergence of whole genera of other taxa. So it is useful to group the Placozoa into phylogenetic subunits. I mentioned that the approved definition of species can not be used for Trichoplax yet, so the different 16S-varieties are referred to as haplotypes. The most important one is H1, because the whole genome is sequenced. This haplotype was collected by Karl Grell (so it is called "Grell-clone" in laboratory jargon) in the 1970s at the Red Sea. After the cultivation of these specimens they were used for scientific work all over the world.

Another interesting haplotype is H2, which exceptionally was found at the coast of Roscoff France in the cold Atlantic. The sequencing of this genome is still in progress. Advantages in cultivating H2 are the robustness against outside influences like temperature or salinity.

Also interesting is the haplotype 16, which was found near Kenya in 20m depth. This is the maximum depth *Trichoplax* was ever found. Admittedly, it is not easy to cultivate or work with H16. Last point is due to the exceptional high density of cilia this haplotype has which makes it hard loosen it off from surfaces without damaging it.

Ecology

The 16 haplotypes known today are further organized in seven clades (figure 1), which are distributed differently. For example clade I was found ubiquitary all over the world (up to 50 degrees northern and southern latitude) whereas the clades II and III are only found at latitudes near the equator. Regarding this it can be speculated, that the different haplotypes use different ecological niches or have at least different requirements to their habitat.



Figure 1: The phylogenetic groups of Trichoplax adhaerens. The 16 haplotypes are organized in seven clades. The genetic distance is shown at the bottom of the figure. After Schierwater et al. (2010), edited.

The position in the Tree of Life

An elemental question of humanity is where their origin is. Different approaches to reconstruct the Tree of Life are retraceable up to the beginnings of biological science.

In order to reach high plausibility for the Tree of Life it is necessary to use multidisciplinary tools. Schierwater et al. (2009a) used multigene analyses (including Hox-genes, mitochondrial DNA, ribosomal RNA) for creating a tree (figure 2), where Diploblasta and Bilateria are sister groups. At the base of the Diploblasts we find the Placozoa as a sister group to the aggregate of Porifera and Coelenterata.

The most basal metazoan position of the Placozoa is underlined by the expression of Hox-genes, relating to the placozoan and cnidarian bauplan. These expression patterns approve the placula hypothesis (Bütschli 1884). Thus a amoeboid urmetazoon, lacking any form of axis or symmetry, began to raise the central point of its disk-shaped body, gaining a cavity. The cavity could be turned into a digestion cave (like cnidarian gastrovascular system) or into a water flow system (like Porifera possess).



Figure 2: Phylogenetic tree with relationship of Coelenterata, Porifera, Placozoa and Bilateria. 16S-ribosomal RNA and Hox-Genes were used. After Schierwater et al. (2009c), edited.

The invention of nervous system

Some classical hypothesis say that the nerve cells evolves only one time (Borchiellini et al. 2008), so all taxa with nerve cells are monophyletic. An often mentioned argument for this is the simplicity. But this can be refused by including the gradual development of nerve cells (Schierwater et al. 2009c), under precondition that the last common metazoan ancestor has some rudimental qualities of nerve cells (like stimulus perception cells). This gradual evolution approves a simple way of convergence referred to nervous systems.

Conclusion

The arguments and data I presented report of a phylum, that at first sight looks very simple. Only on closer examination the Placozoa show their great diversity. Genetic and morphological evidences suggest that the Placozoa are the most basal metazoan Phylum within the Tree of Life, therefore *Trichoplax adhaerens* is the most probable candidate for being "the mother of all metazoan".

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References

1. Borchiellini C., Manuel M., Alivon E., Boury-Esnault

N., Vacelet J., Le Parco Y. (2008): Sponge paraphyly and the origin of Metazoa, Journal of Evolutionary Biology, Volume 14, Issue1, p.171-179

- 2. Bütschli (1884): Bemerkungen zu Gastrea-Theorie, Morph, Volume 9, p.415-427
- de Queiroz K. (2005): Ernst Mayr and the modern concept of species, Proc Natl Acad Sci USA, Volume 102, p.6600-6607
- Delsuc F., Brinkmann H., Philippe H. (2005): Phylogenomics and the reconstruction of the tree of life, Nature Reviews Genetics, Volume 6, p.361-375, retrieved from:
- Grell K., Benwitz G (1974): Elektronenmikroskopische Beobachtungen über das Wachstum der Eizelle und die Bildung der "Befruchtungsmembran" von Trichoplax adhaerens F. E. Schulze (Placozoa), Zoomorphology, Volume 79 p295-310
- Jackson A., Buss L. (2009): Shiny spheres of placozoans (Trichoplax) function in anti-predator defense, Invertebrate Biology, Volume 128 Issue 3, p.205-212
- Kimbel W., Johanson D., Rak Y. (1994): The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia, Nature, Volume 368, p.449-451
- Müller W., Wiens M., Adell T., Gamulin V., Schröder H., Müller I. (2004) Bauplan of Urmetazoa: Basis for Genetic Complexity of Metazoa, International Review of Cytology, Volume 235, p.53-92
- 9. Schierwater, B. (2005): My favorite animal, Trichoplax adharens, BioEssays, 27.12, p.1294-1302
- Schierwater B., Eitel M., Jakob W., Osigus H., Hadrys H., Dellaporta S., Kolokotronis S., DeSalle R. (2009a): Concatenated Analysis Sheds Light on Early Metazoan Evolution and Fuels a Modern "Urmetazoon" Hypothesis, PloS Biology
- Schierwater B., de Jong D., Desalle R. (2009b): Placozoa and the evolution of Metazoa and intrasomatic cell differentitation, Int J Biochem Vell Biol. Volume 51, p.370-379
- Schierwater B., Kolokotronis S., Eitel M., DeSalle R. (2009c): The Diploblast-Bilateria Sister hypothesis, Communicative & Integrative Biology, Volume 2, Issue 5, p.1-3
- Schierwater B., Eitel M. (2010): The phylogeography of the Placozoa suggests a taxon-rich phylum in tropical and subtropical waters, Molecular Ecology, 19, p.2315-2327
- Signorovitch A., Dellaporta S., Buss L. (2005): Molecular signatures for sex in the Placozoa, Proc Natl Acad Sci USA, Volume 102, p.15518-15522
- Srivastava M., Begovic E., Chapman J., Outnam N., Hellsten U., Kawashima T., Kuo A., Mitros T., Salamov A., Carpenter M., Signorovitch A., Moreno M., Kamm K., Grimwood J., Schmutz J., Shapiro H., Grioriev I., Buss L., Schierwater B., Dellaporta S., Rokshar D. (2008): The Trichoplax genome and the nature of placozoans, Nature 454, p.955-960