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## A CLARIFICATION ON: "GALLERTOID" AND "BENTHOBLASTAEA-BILATEROGASTRAEA" AS PREFERABLE MODELS FOR METAZOAN EVOLUTION

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This is an addendum to "*Trichoplax adhaerens*: discovered as a missing link, forgotten as a hydrozoan, re-discovered as a key to metazoan evolution" by T. Syed and B. Schierwater, *Vie et Milieu/Life & Environment* 52/4: 177-187 (2002b). The aim of this article was to "review the history of research on *Trichoplax*, and provide a modern interpretation of special *Trichoplax*-features in an evolutionary context" (cited from abstract). Unfortunately, the printing version differs from the submitted manuscript, especially section V changed in a way making the original line of argument unclear. In this section, it was intended to explain why the gallertoid-hypothesis by Bonik *et al.* (1976) and the benthoblastaea-bilaterogastraea by Jägersten (1959) are among the preferable models for metazoan evolution. The point is that both models describe an early connective tissue which serves for mechanical stabilization, and that the form-controlling function of the interior fibre cells of *Trichoplax* supports these reconstructions. This latter idea was introduced during the discussion of Bütschli's placula-hypothesis (p. 185):

*"Bütschli regarded the three-layered Trichoplax as derived from the two-layered placula. This is another critical point of the placula-hypothesis, because it is not straightforward how the interior fibre cells could have emerged from a two-layered construction."*

In the final version of the manuscript, the continuation of the text was as follows:

*"We want to stress here that in general the assumption of early metazoan forms without inner form-controlling elements, such as a hollow "blastaea" which becomes a flattened "benthoblastaea", is quite unrealistic from a biomechanical point of view (compare also Bonik *et al.* 1976, 1978; Gutmann 1989). The recent *Trichoplax adhaerens* is a good model to support this critique: Starving*

*placozoans change from their normal, flattened shape to a spherical form, as the interior fibre cells degenerate and lose contact with the epithelia. These starving forms are not able to regenerate and soon die (see also Thiemann & Ruthmann 1990). Thus, we think that Jägersten's (1959) improved description of the benthoblastaea, as cited in IV, and the gallertoid as proposed by Bonik *et al.* (1976) are the most preferable models of early metazoans. Any models which ignore the importance of connective tissue in the animal realm should be replaced."*

Furthermore, the proposed explanation for eventually preferring the gallertoid-model was as follows:

*"When comparing the gallertoid-hypothesis with Jägersten's benthoblastaea-bilaterogastraea scenario, there is one important difference regarding the evolution of placozoans. In Jägersten's model, the early benthic metazoans develop an antero-posterior polarity before transforming to the bilaterogastraea-stage (comp. Fig. 4). It is difficult to understand why placozoans, which evidently have to be derived from a benthoblastaea-like stage, did not develop an A/P-axis then, or which were the selective forces that separated these two lines. It is even more inappropriate that placozoans are often named as model organisms for the benthoblastaea-bilaterogastraea transition because of their behaviour of bulging while digesting large food particles, which was suggestively called "temporary gastrulation" by Grell. In fact, *Trichoplax* obviously did not develop a gut or an A/P-axis during probably a billion years of benthic existence. Therefore, we prefer the alternative as shown in Fig. 5, a model which clearly separates placozoan evolution from the bilateria or, in general, from phyla with inner canal systems: placozoans emerge from benthic vagile precursors, while organisms with interior canals developed in the pelagic (see also Syed & Schierwater 2002a)."*

Instead of the argumentation given above, the printed version mentions hollow amphiblastula-larvae of some poriferan species, which flatten and infold after settling. This was an interesting hint by one of the referees, since these larvae – or sponges in general – do not possess interior contractile cells comparable to placozoan fibre cells. In fact, we here face a good example why ontogenetic processes, in contrast to wide-spread opinion, may not be suitable for the explanation of evolutionary transformations. The morphogenetic movements of blastula-like embryonal stages, for example the gastrulation process, are mediated by rearrangements of cell-cell-connections and cytoskeletal elements (cf. Wolpert 1998). Obviously, these mechanisms cannot explain evolutionary transformations of benthic-vagile metazoans, as they are discussed in the case of gradually flattening benthoblastaeae or gallertoids. Instead, connective tissue-like elements determine form-controlling forces in adult metazoans, which means that any change of form during evolution depends on gradual reorganisation of these decisive structures. Modern reconstructions of metazoan evolution should take this biomechanical aspect into account.

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