

***Interactive comment on* “The unique skeleton of siliceous sponges (Porifera; Hexactinellida and Demospongiae) that evolved first from the Urmetazoa during the Proterozoic: a review” by W. E. G. Müller et al.**

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Title. "Urmetazoa" is not an officially accepted name in the scientific community, as the title might suggest. There is no requirement to give names to hypothetical common ancestors of monophyla. On the contrary, one should not do so because they could be confused with taxon names (a hypothetical ancestor is not a taxon).

Answer: We have to consider that the term Urmetazoa is introduced in the public (Google) with over 749 citations and in the literature with 2499 (PubMed) - and this

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term is established like the term Urbilateria. So I will stick to this term.

Reply: I do not agree that "Urmetazoa" is an established term. As a systematic zoologist reading systematics literature and communicating with other systematists I must say that this term is very rarely used. A little search on Google Scholar and journal websites for "Urmetazoa" shows that this term is almost never mentioned in the most relevant journals for the fields of Evolution and Systematics: Systematic Biology, Trends in Ecology and Evolution, Trends in Genetics, Evolution, Cladistics, Molecular Phylogenetics and Evolution, Proceedings of the Royal Society B, Philosophical Transactions of the Royal Society B, Zoological Journal of the Linnean Society, Biological Journal of the Linnean Society, Journal of Evolutionary Biology, Zoologica Scripta, Acta Zoologica, as well as Nature, Science, PNAS, and PLoS Biology, all yielded zero (0) matches. There is 1 paper in Molecular Biology and Evolution, 1 in Journal of Zoological Systematics and Evolutionary Research, 1 in Evolution and Development, and 6 in Journal of Molecular Evolution containing this term. Of these 9 papers, 7 come from Prof. Müller's group. I think these results speak for themselves. Besides, the fact that a term is cited so-and-so often is not a scientific justification for its use.

Abstract - p. 386, l. 1-2; l. 7-8 First, it is not Porifera itself, but its phylogenetic position that might have been "enigmatic". Second, it is not true that the phylogenetic position of sponges was unclear before the analysis of their genetic repertoire, or that molecular studies demonstrated "that all metazoan phyla, including the Porifera, originate from one common ancestor". In fact, monophyly of Metazoa is well supported by several non- molecular characters such as extracellular matrix and sperm ultrastructure (see Ax, 1995). Molecular data only provided further support for this hypothesis.

Answer: This is not so correct: Please see the paper: Reitner J, Schumann-Kindel G, Thiel V: Origin and early fossil record of sponges - a geobiological approach. Memoire of the Queensland Museum 44: 515, 1999. There one can read: "As an hypothesis, sponges originated from biofilms which were associated with choanoflagellates". So we see the need to say that the "enigmatic" period was overcome by molecular studies.

In the very outstanding book of Ax the monophyly is also proposed - but the molecular biological part of this volume is weak. Just to mention: the book of Ax appeared 1995 and our articles on the monophyly appeared earlier: Müller WEG, Müller IM, Gamulin V (1994) On the monophyletic evolution of the Metazoa. Brazil. J. Med. Biol. Res. 27: 2083-2096; and Müller WEG, Müller IM, Rinkevich B, Gamulin V (1995) Molecular evolution. Evidence for the monophyletic origin of multicellular animals. Naturwiss. 82: 36-38 The author Ax refers to our paper. Therefore, the argumentations of the geo-biological colleague is ambiguous.

Reply: I am well aware of Prof. Reitners faible for biofilms and his hypothesis that sponges evolved from such structures. However fascinating this idea might be, considering the overwhelming evidence in favor of metazoan monophyly, it would require either a very unparsimonious explanation for animal origins (from a cladistic viewpoint, namely polyphyly of Metazoa), or imply that not Porifera, but Metazoa as a whole evolved from biofilms. Besides, the cited paper is from 1999, whereas Prof. Müllers papers on metazoan monophyly are - as he mentions further below - from 1994 and 1995. Therefore, the argumentation that the paper of Reitner et al. demonstrates that "the enigmatic period was overcome by molecular studies" suffers from a logical flaw. Regarding the comments on the book of Prof. Ax, I have to mention that the characters listed as autapomorphies of Metazoa on p. 53 were not reported for the first time in that book; "Das System der Metazoa" is a synthesis. Therefore, it is not relevant if it was published one year after Prof. Müller's paper. I have to admit, however, that Prof. Ax is not so generous with references - perhaps because he perceived the question of the phylogenetic position of Porifera as not particularly enigmatic or metazoan monophyly as a widely accepted hypothesis. Furthermore - as pointed out by Prof. Ax on p. 50 - the scope of the taxon "Metazoa" already included Porifera when it was originally introduced by Haeckel in 1874. In any case, non-molecular evidence for metazoan monophyly is substantial, and it is not good scientific behaviour to conceal this in a review article and only present ones own results.

- p. 386, l. 19, and elsewhere in the manuscript According to Systema Porifera (Hooper and van Soest, 2002; see also the Porifera Database at <http://www.vliz.be/vmdcdata/porifera/index.php>), Monorhaphis currently includes only one species, *M. chuni*.

Answer: I cannot follow the reader: In “Systema Porifera” is only reported that *M. chuni* and *M. intermedia* are the same species - no reasons are given for this. The only - perhaps valid - contribution is from Tabachnik KR, Lévi C (2000) Porifera: Hexactinellida: Amphidiscophora off New Caledonia. *Mém Muséum National d’Histoire Naturelle* 184:53-140. There it is only mentioned that both species have the same “types of spicules”. Again no more data are given. This is for me too weak to bring these two species to one.

Reply: The chapter in Systema Porifera on Monorhaphididae by Dr. Tabachnik is the latest revision of that taxon. Since Dr. Tabachnik is one of the world-leading authorities in hexactinellid taxonomy (and the number one authority in taxonomy of Amphidiscophora), any scientist who is not specialised in the taxonomy of the group (like Dr. Müller) should stick to his classification. Furthermore, Dr. Tabachnik has a reputation of being a "splitter" as a taxonomist, so when he lumps three species to one, this really means something.

- p. 387, l. 24 Where is the evidence that silicon triggered the "emergence" of sponges? There are sponges with calcareous skeletons and sponges with no mineral skeletons at all, and they are quite successful, too.

Answer: I would like to refer to the paper "Krasko A, Schröder HC, Batel R, Grebenjuk VA, Steffen R, Müller IM, Müller WEG (2002) Iron induces proliferation and morphogenesis in primmorphs from the marine sponge *Suberites domuncula*. *DNA & Cell Biol.* 21: 67-80". There the morphogenetic potential of silicon is first outlined.

Reply: As far as I understand it, this paper is more about iron than about silicon. Maybe Krasko et al. (2000): *Eur. J. Biochem.* 267:4878 is a more appropriate reference?

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In any case references should be given. Also, it was not my intention to question that silicon "comprises morphogenetic and also structural properties". I just do not see conclusive evidence that silicon triggered the evolution of sponges, i.e. where is the evidence that the ability to produce siliceous spicules was the major adaptive advantage responsible for the success of sponges? It might well have been so, but we can only speculate about it. Maybe filter feeding was the key trait.

- p. 388, l. 5 The term "crown taxon" is wrongly used here. All extant taxa, including sponges, are crown taxa (as opposed to stem taxa, which are extinct members of a lineage).

Answer: I will stick to this term "crown taxon" - since I wrote it in quotation marks. AND this term is found both in monographs and original papers, e.g. Evolutionary relationships among the eukaryotic crown taxa taking into account site-to-site rate variation in 18S rRNA by; Van De Peer, Y. ; De Wachter, R. ;

Reply: First, putting a wrongly used term in quotation marks does not make it correct (besides, it is not put in quotation marks throughout the article). Second, of course the term can be found in the literature. It is a valid scientific term - if correctly applied. If one looks at the phylogeny of a lineage that includes extant and extinct taxa, then the extant taxa are referred to the crown group, and the extinct taxa to stem groups. However, sponges are not extinct, so they are members of a metazoan crown group, just as vertebrates. The term "crown group" can only be applied when extant and fossil taxa of a lineage are compared.

- p. 388, l. 6-7 How exactly does silicon cause gene expression? Where is the evidence or reference for this proposed mechanism?

Answer: The geo-biological colleague is asked to look in the papers of the main author; e.g.: Krasko A, Schröder HC, Batel R, Grebenjuk VA, Steffen R, Müller IM, Müller WEG (2002) Iron induces proliferation and morphogenesis in primmorphs from the marine sponge *Suberites domuncula*. DNA & Cell Biol. 21: 67-80; OR: Müller WEG, Wiens

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M, Adell T, Gamulin V, Schröder HC, Müller IM (2004) Bauplan of urmetazoa: Basis for genetic complexity of Metazoa. Intern. Review of Cytology 235: 53-92; OR: Müller W.E.G. (2006) The stem cell concept in sponges (Porifera): metazoan traits. Seminars in Cell & Develop. Biol.17: 481-491.

Reply: I am grateful to Prof. Müller for pointing out to me where the requested evidence can be found in the literature. I'm sure, however, that other readers of his review article would also like to know it.

- p. 388, l. 9-11 I do not agree that spicules are the "key structures allowing the formation/arrangement of the differentiated cells ... according to a body plan". Sponges without spicules also have a body plan.

Answer: I absolutely disagree with this comment. A body plan is established by an axis. The first paper on this subject came from our groups; please see: "Wiens M, Belikov SI, Kaluzhnaya OV, Krasko A, Schröder HC, Perovic-Ottstadt S, Müller WEG (2006) Molecular control of serial module formation along the apical-basal axis in the sponge *Lubomirskia baicalensis*: silicateins, mannose-binding lectin and Mago Nashi. Dev. Genes & Evol. 216: 229-242".

Reply: I understood "body plan" in a more general sense. Maybe Prof. Müller's definition should be more explicitly stated in the article.

- p. 388, l. 23 - p. 389, l. 1 The use of the terms "macroevolution" and "microevolution" in this section is a bit confusing. I think what the authors are trying to introduce here are the concepts of the origin of evolutionary novelties by either a) accumulation of gradual changes or b) saltatorial changes. However, they fail to do so in an understandable manner. Anyway, I do not see the relevance for the article of introducing these concepts in the first place. It does not matter in this context if the discussed evolutionary novelties arose by one or the other mechanism.

Answer: No. The terms "macroevolution" and "microevolution" have been discussed

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earlier; please see: Mayr E (2001) What Evolution is. Basic Books, New York.

Reply: I know that these terms have been discussed earlier and I don't criticise the terms as such. I just want to point out that they are used here in a very confusing way and that they need not be introduced at all in the context of the article. So, to avoid confusion and make the article more readable it would be appropriate to avoid them.

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