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***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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As an evolutionary biologist, I have to point out that this manuscript contains numerous unclear formulations, cases of wrongly used terminology, unsubstantiated or simply false statements, contradictions, and errors. Also, published work relevant to the subject is ignored. Besides, this article is not well written and the English needs improvement. Here are my detailed comments:

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"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).

#### 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.

- 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*.

#### Introduction

- p. 387, l. 6-8

See comment above.

- p. 387, l. 23

The formulation "factors which allowed the evolution" is very vague. Specifically, it is not quite clear if the authors are referring to the "origin" or the "radiation" of sponges ("evolution" could mean both).

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- 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.

Role of silicon and silicate

- 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).

- p. 388, l. 6-7

How exactly does silicon cause gene expression? Where is the evidence or reference for this proposed mechanism?

- 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.

- p. 388, l. 15-20

It is not clear to me what the authors are trying to say with the second part of the sentence starting with "This finding ...". Why was it not anticipated? It is obvious that the spicules are the "structural basis" for these sponges. This sentence does not make any sense.

Evolution during the Proterozoic: evolution of sponges in the silicon ocean

- 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

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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.

- p. 389, l. 4

This statement is completely redundant. Metazoan monophyly is well supported and was well supported before molecular data became available (see above). So, by definition all metazoans emerged from their most recent common ancestor.

- p. 389, l. 7-8

The Ediacaran biota is not considered part of the Cambrian Explosion; it predated it.

- p. 389, l. 10-11

First, it should read "metazoan phylum" or "animal phylum". Second, other animal phyla were certainly already around at the Neoproterozoic/Cambrian boundary. The authors should not simply claim that sponges were dominant or even the sole phylum at that time, but discuss this in more detail and provide references.

- p. 389, l. 12

Sponges are not "living fossils". Most researchers would define a living fossil as a relict taxon that is still alive today whereas all of its close relatives (members of the same ancient radiation) went extinct long time ago. Perhaps the term should be avoided altogether in a rigorous scientific context. In any case, sponges are very widespread and diverse today and play major ecological roles, so they are certainly not relicts of an ancient radiation. Therefore, the term "living fossil" does not apply to them.

- p. 389, l. 15-17

References are missing for the times of occurrence and possible extent of these glacia-

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tions.

- p. 390, l. 4

The sponges described in Li et al. (1998) were referred to Demospongiae, so this reference is out of place here.

- p. 390, l. 4-5, l. 22 ff.; p. 391, l. 11 ff.

Demosponge fossils have been found in 750 my old strata of Nevada (Reitner and Wörheide, 2002), so demosponges predate hexactinellids in the known fossil record.

- p. 391, l. 7-10

What relevance does the age of freshwater sponges have to the issues addressed in this review?

- p. 391, l. 27-29

References are missing for the environmental conditions during that period.

- p. 392, l. 15-18

The authors do not explain why soluble silicate should have provided a basis for survival and diversification. Evidence and/or references are missing.

- p. 392, l. 22-24

References or evidence are missing for this hypothesis.

- p. 392, l. 25-29

This section is unclearly written, and references are missing. What does "genetic toolkit for all deriving metazoans" mean? What are "deriving metazoans" anyway? Why does the genetic repertoire of sponges "gives the frame" etc. of the body plan construction seen in "higher groups" ("crown groups" is wrong; see above)? If at all, it is the genetic repertoire of the common ancestor of sponges and eumetazoans that set the limits of

animal body plan construction.

- p. 393, l. 1

Again, "crown taxa" is the wrong term (see above).

- p. 393, l. 2-5

I think science should not be a matter of postulating things but testing hypotheses in the light of observations. What does "entropy" mean in an evolutionary context? "Complexity" is also a rather vague term, and besides it is well known that simplifications have occurred during the course of evolution. The term "perfection" should be avoided in an evolutionary context since it implies an underlying "plan", which puts things in the realm of creationism. Anyway, it is not clear to me what this sentence is supposed to mean. Why should increased complexity be detrimental to the survival of younger species? What species are the authors referring to, and younger than what are these species supposed to be?

Unique formation and degradation of biomaterial (biosilica) in sponges: silicatein and silicase

- p. 393, l. 23

What relevance do cnidarians have in this context? What do the authors mean by "the major evolutionary transitions to the Porifera and Cnidaria"? This sentence is rather confusing.

- p. 393, l. 24-26

As stated above, there are also sponges without spicules, and they have a body plan, too. Besides, spicules and sclerocytes are not the same: the former are products of the latter, and sclerocytes as such do not stabilize the sponge body.

Hexactinellida: first approaches to understand spicule formation

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- p. 396, l. 14

Hexactinellid microscleres generally don't fuse, in both subclasses. Besides, this is totally irrelevant to the context of this paragraph.

- p. 396, l. 15-16

Monorhaphididae currently contains only a single species, *M. chuni* (see above).

- p. 397, l. 5

The citation is clearly in the wrong place here. The species was not described in the cited reference, and there is also nothing else in this sentence that relates to the reference, except the species itself.

- p. 397, l. 23

I'm sure for non-spongiologists "comitalia" is certainly not a well-known term; an explanation is missing.

Demospongiae: silica deposition during spicule formation

- p. 398, l. 17-18

The morphology of sponge spicules has been analyzed before. This sentence should therefore read "the morphology of the spicules of *S. domuncula* has been analyzed recently". However, the morphology (external shape) of these spicules was known before; what is important here is the internal structure and mode of formation, not the morphology.

- p. 398, l. 24

TEM stands for "transmission electron microscopy", not "transmission microscopical analysis".

Figure 1

In Fig. 1 C, the whole sponge is pictured, not only the giant spicule, as stated in the figure caption.

## Figure 2

First, see comment on "Urmetazoa" above. Second, what is the difference between the light blue bars and the dark blue bars and what does the height of the bars mean (i.e., how is the y-axis scaled?). Third, it should be "years before present", not "Years". Fourth, according to the figure, metazoans evolved about 900 my ago (and the so-called "Urmetazoa" even earlier), whereas in the figure caption it is stated that they evolved between 600 and 800 my ago. Finally, the Neoproterozoic does not continue up to the present day (0 years) as implied by the figure (what happened to the Phanerozoic?).

## Figure 3

### Figure

First, see the above comments on "living fossils" and "Urmetazoa" (this applies also to "Urbilateria"). Second, the phylogenetic position of Archaeocyatha is still being debated; certainly they are not the sister group of Eumetazoa, as implied by this tree. Third, the "silicic acid skeleton" is very likely an autapomorphy of siliceous sponges (and not of Metazoa as the figure implies); the "Ca-carbonate skeleton" (spicules to be precise; see below) is an autapomorphy of Calcarea (not of Calcarea+Eumetazoa), "oral/aboral axis" and "radial symmetry" are probably autapomorphies of Cnidaria (not of Eumetazoa), and "biradial symmetry" certainly is an autapomorphy of Ctenophora (not of Ctenophora+Bilateria). Fourth, a number of demosponge groups are also capable of secreting Ca carbonate skeletons, whereas Ca carbonate spicules only occur in Calcarea. Finally, this tree displays Hexactinellida+Demospongiae as monophyletic (which I agree with), but in the section "Evolution during the Proterozoic: evolution of sponges in the silicon ocean" the authors state that Hexactinellida is the oldest group of sponges. If Hexactinellida and Demospongiae are sister groups, one cannot be older



than the other.

### Figure caption

First, see above comments on "Urmetazoa", "Urbilateria", and "living fossils". Second, in l. 4-6, the expressions "emerged first" and "finally ... appeared" are very vague and not in good agreement with modern phylogenetic terminology. Also, sponge paraphyly is still being debated. Third, I am not aware of any study that recovered Calcarea as "a sister group of the Cnidaria" (l. 8); the current working hypothesis in the molecular phylogenetics community appears to be that Calcarea is the sister group of Eumetazoa. Fourth, ctenophorans did certainly not "evolve from" cnidarians (l. 8-9). This would imply that Cnidaria is paraphyletic, which is very unlikely. Ctenophora is either the sister group of Bilateria, of Cnidaria, or of Cnidaria+Bilateria; there is currently no consensus regarding these three hypotheses. Fifth, references are missing for the phylogenetic hypotheses and for the hypothesis that metazoans evolved between the Sturtian and the Varanger-Marinoan glaciations (l. 11-12). Finally, it is not explained what the green triangles in the figure mean.

### Figure 5

This is not a radial tree, as stated in the figure caption, but an unrooted phylogram. What tree-reconstruction method (implemented in which software under which settings) was used? What does the scale bar stand for?

### References

Ax, P. 1995. *Das System der Metazoa I*. Fischer, Stuttgart, Jena, New York.

Hooper, J. N. A., and R. W. M. van Soest. 2002. *Systema Porifera. A Guide to the Classification of Sponges*. Plenum, New York.

Reitner, J., and G. Wörheide. 2002. Non-lithistid Demospongiae - origins of their palaeobiodiversity and highlights in history of preservation. Pages 52-68 in *Systema Porifera. A Guide to the Classification of Sponges* (Hooper, J. N. A., and R. W. M. van

Soest, eds.). Plenum, New York.

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