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Biogeosciences Discussions

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.

W. E. G. Müller et al.

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From : Prof. Dr. W.E.G. Müller, Institut für Physiologische Chemie, Abteilung Angewandte Molekularbiologie, Universität, Duesbergweg 6, 55099 Mainz; GERMANY. tel.: +49-6131-392-5910; fax.: +49-6131-392-5243; E-mail: wmueller@uni-mainz.de

To the Editorial Board

MS-NR: bgd-2006-0069

Dear colleagues:

Thank you for your email from April 2nd informing me that our manuscript entitled:

The unique skeleton of siliceous sponges (Porifera; Hexactinellida and Demospongiae) that evolved first from the Urmetazoa during the Proterozoic: a review by:

Werner E.G. Müller, Jinhe Li, Heinz C. Schröder, Li Qiao and Xiaohong Wang

which we submit for the Journal Biogeosciences must be revised.

In the following we discuss point for point the arguments raised by the referees/reader. In detail:

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. By: M. Dohrmann, mdohrma1@gwdg.de

General comment: 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. Answer: The English will be corrected - the remarks of the geo-biological colleague will be considered.

Here are my detailed comments:

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

BGD

4, S262–S276, 2007

Query: 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.

Query: - 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

BGD
4, S262–S276, 2007

EGU

weak to bring these two species to one.

Query: Introduction - p. 387, l. 6-8 See comment above. Answer: Does the geo-biological colleague want to stress that our statement “The origin of the first ancestor of all metazoan phyla remained enigmatic until the first sequences coding for informative proteins from a sponge (phylum Porifera) had been identified by application of molecular biological techniques Pfeifer et al., 1993)“ does not reflect real situation? If he disagrees - then please give conclusive references.

Query: - 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). Answer: Will be corrected accordingly.

Query: - 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. 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.

Query: - 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 if 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. ;

Query: - 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

BGD

4, S262–S276, 2007

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 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.

Query: - 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”.

Query: - 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. Answer: The English will be polished.

Query: 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 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 "macroevo-

BGD
4, S262–S276, 2007

Interactive Comment

EGU

lution" and "microevolution" have been discussed earlier; please see: Mayr E (2001) What Evolution is. Basic Books, New York.

Query: - 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. Answer: I ask the reader to give me a valid publication where this is outlined un-ambiguously. I refer to the article of Rodrigo et al (Are sponges animals? An investigation into the vagaries of phylogenetic inference). In: Sponges in Time and Space (1994).

Query: - p. 389, l. 7-8 The Ediacaran biota is not considered part of the Cambrian Explosion; it predated it. Answer: We will correct accordingly.

Query: - 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. Answer: We will include “metazoan phylum” and will outline that sponges had been the sole phylum with a hard skeleton.

Query: - 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. Answer: Sponges as "living fossils". I will stick to this term, since it is also used in the group of the reader: “Jahn, T., König, G.M., Wright, A.D., Wörheide, G. Reitner, J. (1997): Manzacidin D: An Unprecedented Secondary Metabolite from the ĎLiving Fossil“ sponge Astrosclera willeyana.- Tetrahedron Letters, 38: 3883-3884.”.

BGD

4, S262–S276, 2007

Query: - p. 389, l. 15-17 References are missing for the times of occurrence and possible extent of these glaciations. Answer: Will be given: [Hoffmann, P. A. and Schrag, D. P.: The snowball Earth hypothesis: testing the limits of global change, Terra Nova, 129-155, 2002.] This reference is already in the reference list.

Query: - p. 390, l. 4 The sponges described in Li et al. (1998) were referred to Demospongiae, so this reference is out of place here. Answer: We will change.

Query: - 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. Answer: The reader perhaps refers to: Reitner, J. & Wörheide, G. (2002): Non-Lithistid fossil Demospongiae - Origins of their Palaeobiodiversity and Highlights in History of Preservation.- In: Hooper, J.N.A. & Van Soest, R. (eds.), Systema Porifera: A Guide to the Classification of Sponges. 52-68 (Kluwer) New York. If I see it correctly, this review only states the existence of those sponges, without giving photos or any other detailed data. If so, the evidence is not enough for me.

Query: - p. 391, l. 7-10 What relevance does the age of freshwater sponges have to the issues addressed in this review? Answer: It should highlight that the freshwater sponges evolved later. This appears not to be necessary - however I want to refer to the hot discussion about the origin of the endemic sponges in the Lake Baikal.

Query: - p. 391, l. 27-29 References are missing for the environmental conditions during that period. Answer: We will refer to: Butterfield NJ (2007) Macroevolution and macroecology trough deep time. Palaeontology 50. 41-55.

Query: - 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. Answer: Please see: Müller WEG, Schröder HC, Wrede P, Kaluzhnaya OV, Belikov SI (2006) Speciation of sponges in Baikal-Tuva region (an outline). J. Zool. Syst. Evol. Research 44: 105-117. There we outlined that silicatein, the basic protein

BGD
4, S262–S276, 2007

EGU

which produces silica in sponges, diversified in freshwater sponges and might be highly correlated with the evolution of the Lake Baikal sponges.

Query: - p. 392, l. 22-24 References or evidence are missing for this hypothesis. Answer: I will include in the sentence: “Hence, the sponges (survivor taxon) became the beneficiaries of the glaciation crises and received the chance to colonize those habitats which had been de-populated.” The reference of Butterfield NJ (2007) Macroevolution and macroecology trough deep time. Palaeontology 50. 41-55, will be included. However, the basic concept - we think - has been outlined in the presented review.

Query: - 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. Answer: If I understand the reader correctly wants that I give as a reference to that paragraph the citation of: “Pilcher, H.: Back to our roots, Nature, 435, 1022-1023, 2005.”. There, these terms are outlined and also the term “Urmetazoa” has been highlighted.

Query: - p. 393, l. 1 Again, "crown taxa" is the wrong term (see above). Answer: See above.

Query: - 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

BGD

4, S262–S276, 2007

than what are these species supposed to be? Unique formation and degradation of biomaterial (biosilica) in sponges: silicatein and silicase. Answer: In a review it is allowed to speculate in order to provide the ground for further scientific contributions. I refer to our paper (Müller WEG, Müller IM (2003) Analysis of the sponge [porifera] gene repertoire: Implications for the evolution of the metazoan body plan. In: Marine Molecular Biotechnology (Müller WEG, ed.) Springer-Press, Berlin, pp. 1-33) in which we also provide data that sponges have over 100,000 gene in contrast to the 34,000 genes in human. If they are expressed - which must be checked - then the diversity of transcripts might be higher in sponges than in humans. How to explain that? - only by redundancy? Perhaps I will exchange "entropy" by “redundancy”.

Query: - 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. Answer: OK, I will omit the Cnidaria.

Query: - 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 Answer: I cannot follow the argumentation of the reader. Please find in the article of “Reitner, J. & Wörheide, G. (2002) [see above]” the outline: “The origin of the sponge bodyplan is probably related to the development of special stromatolite-forming biofilmsĚ.”. Is this what the reader means with bodyplan?

Query: - p. 396, l. 14 Hexactinellid microscleres generally don’t fuse, in both subclasses. Besides, this is totally irrelevant to the context of this paragraph. Answer: He is correct - I will change.

Query: - p. 396, l. 15-16 Monorhaphididae currently contains only a single species, M. chuni (see above). Answer: I do not agree; see above. No solid arguments have been published yet.

BGD
4, S262–S276, 2007

EGU

Query: - 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. Answer: OK; we will omit “(Müller et al., 2006c)” - this reference is used anyhow in other paragraphs of this article.

Query: - 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. Answer: OK - I will include an explanation.

Query: - 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. Answer: We will include: “The biochemical basis for the understanding of the morphology of the spicules of S. domuncula has been analyzed recently”.

Query: - p. 398, l. 24 TEM stands for "transmission electron microscopy", not "transmission microscopial analysis". Answer: Ok, we will correct

Query: Figure 1 In Fig. 1 C, the whole sponge is pictured, not only the giant spicule, as stated in the figure caption. Answer: Will be included.

Query: 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 socalled "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?). Answer: We will give a more comprehensive description in this review, even though we gave the reference “(Hoffmann and Schrag, 2002)”, where

BGD
4, S262–S276, 2007

EGU

everything is described in details.

Query: 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. Answer: "living fossils" and "Urmetazoa". See outlines above.

Second, the phylogenetic position of Archaeocyatha is still being debated; certainly they are not the sister group of Eumetazoa, as implied by this tree. Answer: We will make on this line a Question mark.

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). Answer: We can follow the reader.

Fourth, a number of demosponge groups are also capable of secreting Ca carbonate

BGD

4, S262–S276, 2007

skeletons, whereas Ca carbonate spicules only occur in Calcarea. Answer: We have here submitted a review. I think this is debatable and should not be included in the paper the occurrence of calcite and silica in one sponge - biochemical data are absent.

Query/Answer: Also, sponge paraphyly is still being debated. Answer: I am happy about the statement of the reader.

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. Answer: Yes - I know, we published this first. See: “Schütze J, Custodio MR, Efremova SM, Müller IM, Müller WEG (1999) Evolutionary relationship of metazoa within the eukaryotes based on molecular data from porifera. Proc. Royal Society Lond. B 266: 63-73”.

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. Finally, it is not explained what the green triangles in the figure mean. Answer: The line to the Ctenophora will be marked with a question mark.

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). Answer: The reference will be added - see above.

Finally, it is not explained what the green triangles in the figure mean. Answer: That is easy - and I hope self-explainable: these are the borders of the respective ice periods.

Query: 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? Answer: OK - I will correct.

BGD

4, S262–S276, 2007

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. Anonymous Referee #3 Received and published: 21 February 2007 Manuscript review for: 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, J. Li, H. C. Schröder, L. Qiao, X. Wang

General comment: This article is a fascinating review of the evolution of skeletal formation in the siliceous sponges (classes Demospongiae and Hexactinellida). While the article is well written and appropriate for publication in Biogeosciences, there are a few issues that should be addressed before this article would be suitable for publication.

Query: Abstract Page 386 Line 23 This reviewer has a slight problem with the terminology used in this sentence. The use of the term “axial canal” is somewhat misleading as it implies that the canal is formed prior to the synthesis of the axial filament. Is it not the axial filament that templates the growth of the surrounding silica, and not the silica that templates the growth of the filament? Is there is a historical reason for this specific word use? In the same sentence, “hexactinellida” and “demospongiae” should be changed to “hexactinellids” and “demosponges”. In addition the authors state that the axial filaments of hexactinellids are composed of silicateins, which has never been shown previously. If an article has been published previously, confirming this, then the reference should be cited. It would thus seem more appropriate to simply say something likeˇE Both the silica spicules from hexactinellids and demosponges contain organic axial filaments. Answer: Will be completely corrected and answered accordingly.

Query: Role of silicon and silicate Page 388 Line 9 As stated above, there is no published data that the hexactinellid axial filaments are enzymatic. The text should thus be modified to reflect this. Answer: Oh yes at least partially: Please see our recent papers: Müller WEG, Eckert C, Kropf K, Wang X, Schloßmacher U, Seckert C, Wolf SE,

BGD

4, S262–S276, 2007

Tremel W, Schröder HC (2007) Formation of the giant spicules of the deep sea hexactinellid Monorhaphis chuni (Schulze 1904): electron microscopical and biochemical studies. Cell& Tissue Research; in press (DOI 10.1007/s00441-007-0402-x). Wang X, Li J, Qiao L, Schröder HC, Eckert C, Kropf K, Wang Y, Müller WEG (2007) The giant spicules of the deep sea hexactinellid sponges of the genus Monorhaphis (Hexactinellida: Amphidiscosida: Monorhaphididae). Acta Zoologica Sinica; in press. We will include this reference.

Query: Unique formation and degradation of biomaterial (biosilica) in sponges: silicatein and silicase Page 393 Line 26+ Again, the authors state here that the silica is deposited around the axial canal. How is it possible that an empty space can template the growth of anything? This is the function of the axial filament. The so-called “axial canal” is merely the channel that is left behind if the axial filament has been destroyed. The text should be modified to reflect this. Answer: Basically I agree with the correct statement of the referee - however we must leave room for further studies - and this might suggest a new principle of spicule formation. Perhaps if the referee allows, I would leave it in a less precise statement.

Query: Also, in the title of this section, the word “biomaterial” is incorrectly used. A “biomaterial” is specifically defined as: a natural or synthetic material (such as a polymer or metal) that is suitable for introduction into living tissue especially as part of a medical device. The word “biomaterial” should therefore be deleted here as well as any other place it appears in the manuscript. Answer: The referee refers to: Unique formation and degradation of biomaterial (biosilica) in sponges: silicatein and silicase. We will follow him completely.

Query: Unique formation and degradation of biomaterial (biosilica) in sponges: silicatein and silicase Page 394 Line 2-4 The authors mention that in figure 4A-C, the spicules and their axial canals from fossil sponges exhibit all of their characteristic features. What are these characteristic features? Answer: OK - I mean the morphology and structure. I will elaborate that section better.

BGD

4, S262–S276, 2007

Query: Hexactinellida: first approaches to understand spicule formation Page 397-398 Line 28-1 The authors claim that the spicules from hexactinellids contain specific proteins that 1) cross-react with anti-silicatein antibodies and 2) exhibit proteolytic activity, however no data is shown to support these claims. Since this is a review article, if a published reference cannot be cited, then the supporting data should be included. Answer: We will include the references: Müller WEG, Eckert C, Kropf K, Wang X, Schloßmacher U, Seckert C, Wolf SE, Tremel W, Schröder HC (2007) Formation of the giant spicules of the deep sea hexactinellid Monorhaphis chuni (Schulze 1904): electron microscopical and biochemical studies. Cell& Tissue Research; in press (DOI 10.1007/s00441-007-0402-x). Wang X, Li J, Qiao L, Schröder HC, Eckert C, Kropf K, Wang Y, Müller WEG (2007) The giant spicules of the deep sea hexactinellid sponges of the genus Monorhaphis (Hexactinellida: Amphidiscosida: Monorhaphididae). Acta Zoologica Sinica; in press

Query: Throughout the manuscript the term" hexactinellidan" is used. It should be replaced by "hexactinellid" (see caption of figure 6, for example) Answer: OK - this will be corrected.

Query: Figure 8 What are the knobby structures shown on the spicule surface in figure 8B? These are likely salt crystals arising from inadequate sample preparation. To the non-specialist, this micrograph is very misleading and should be replaced with an artifact-free image. Answer: OK - we will remove this foto and take another one.

We would like to express our thanks the referees for their helpful remarks - and will include those in the revised version. Thanks that you have given us the chance to publish this review in: Biogeosciences.

With best regards, Sincerely yours,

(W.E.G. Müller) [Z:BIOGEOSCI0407]

Interactive comment on Biogeosciences Discuss., 4, 385, 2007.