Interactive comment on “A new conceptual model of coral biomineralisation: hypoxia as the physiological driver of skeletal extension” by S. A. Wooldridge

Anonymous Referee #2

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The BGD discussion paper “A new conceptual model of coral biomineralization: hypoxia as the physiological driver of skeletal extension” by S.A. Wooldridge provides an intriguing perspective on biomineralization processes in scleractinian corals. The main idea of the paper is summarized in Fig. 5 and 6. In the absence of oxygen (night time hypoxia in zooxanthellate corals), glycolysis is propelled by anaerobic fermentation. The products of the fermentation (acetates) are metabolised to oxylates which are suggested as nucleating seed crystals that initiate skeletogenesis (the main novelty of the paper). The author suggest that the observed in the skeleton of zooxanthellate corals dense growth bands represent organo-seed (“dark calcification”) -> fibre (“light-enhanced calcification”) interactions and single coupled is representative of a typical
24h period.

The model is purely conceptual and as such is not supported by new experimental data. Although there are some literature-based evidences that zooxanthellate corals experience hypoxia at night, there are no evidences that oxylates are actually produced. This is very weak point of the proposed model. Oxylates can be readily determined by Raman spectroscopy (e.g., Conti et al. 2012: Journal of Raman Spectroscopy) and detection of this mineral phase in the coral calicoblastic tissue or/and in the skeleton should be a prerequisite to consider this hypothesis plausible. Up to now, it was amorphous calcium carbonate (ACC) that was considered as transient precursor phases in biomineralization (Weiner et al. 2005: Science). ACC was reported from various organisms (e.g., in echinoderms: see most recent publication by Gong et al. 2012: PNAS) and in none of these papers was there evidence of oxylate presence. Nanocomposite structure of biominerals is often considered as evidence of transformation of ACC nanoparticles into long-range coherent crystals (e.g., Gilis et al. 2011: Journal of Structural Biology). This suggests that the process of "seed" formation is continuous and not limited to "dark calcification" phase as suggested by the model.

The model aims to explain general physiological driver of calcareous biomineralization of marine organisms (p. 12638). Although it is discussed mostly for zooxanthellate corals (symbiotic with dinoflagellates), the author states also that "there is little reason to suggest that the fundamental skeletogenesis drivers need differ significantly for non-zooxanthellae corals" (p. 12638). Clearly, regular night/day differences in physiological requirements of two symbiotic partners have impact on calcification dynamics, no matter what calcification model is proposed. However, very regular growth increments occur also in deep-water, azooxanthellate scleractinians. How precisely the "hypoxia model" may explain such regular succession of "seed"/"fibre" interactions in corals living in stable, deep-water (constant darkness) conditions without photosynthetic partners? Growth increments of such deep-water, azooxanthellate scleractinians are very regular no matter from what depths they are collected (e.g., Stolarski
2003: Acta Palaeontologica Polonica, figs. 2, 6, 8). Clearly some conservative, intrinsic process is responsible for cyclic biomineralization, which, however, is not linked with symbiotic relationships with photosynthesizing organisms. Why not to consider as hypothesis the simplest mechanism which would be charging and discharging mineral (ACC) bearing intracellular vesicles? This mechanism would also explain overall nanocomposite structure of biominerals (see also Mahamid et al. 2011: Cell Tissues Organs).

The author includes also far-fetched speculations about significance of the model for understanding of ocean acidification (chapter 4.2.3) and as general calcification mechanism, for explanation of Cambrian "simultaneous" appearance of organized skeletons in many different taxa (chapter 6). There is an extensive literature discussing Cambrian radiation of skeletonized metazoans, including evolutionary arms-race hypothesis or changes in ocean alkalinity (Kempe & Kazmierczak 1994: Bulletin de l’Institut Océanographique). There are also evidences that first biogenic mineralization (appearance of sclerites) long preceded the Cambrian. Moreover, history of life shows there are several events of such seemingly "sudden" appearances of skeletonized taxa (e.g., scleractinians in the Triassic), and, at the same time, presence of non-calcyfying forms (e.g., occurrence of sea anemones in Cambrian: Han et al. 2010: PloSOne). Perhaps, combination of many factors contributed to formation of skeletons by organisms, and perhaps the most complete answer to this problem can be obtained by analysis of geological history, careful studies of skeletal structures, and finally by gene expression patterns and their involvement in calcification mechanisms in modern organisms. Wooldridge’s model is an interesting starting point for discussion but the real discussion can only be continued using hard evidences and new experimental data from the areas outlined above.

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