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### Doctoral Candidate Katarzyna Janiszewska "Skeletal development in micrabaciid corals and the origin of Scleractinia"

The dissertation consists of four chapters, two of which have been published in the *Journal of Morphology* and a third is currently in review in *Lethaia*. I previously reviewed the two chapters (#1, 2) published in the *Journal of Morphology* (one formally and the other informally), and recently formally reviewed the chapter (#4) submitted to *Lethaia*. All four chapters are very high in quality and make innovative and significant contributions to paleontology and evolutionary biology. They use state-of-the-art microscopic techniques to study skeletal morphology in the scleractinian family Micrabaciidae (Cretaceous-Recent) including both fossil and modern skeletons (museum specimens). The family is especially intriguing because of its recently discovered basal position in scleractinian phylogeny, thereby offering unique insight into the origin of scleractinians. In general, Katarzyna Janiszewska's work shows that morphologic data do not disagree with molecular data. Instead, contrary to claims by other authors, careful microscopic analysis of morphology supports the molecular trees, and thereby represents a reliable and insightful tool for reconstructing scleractinian phylogeny. Scleractinian skeletal mineralization is found to be under strong biological control.

#### **Introduction and Summary**

The introductory section is effective at providing the overall rationale for the four dissertation chapters and their interconnections. In addition to summarizing the chapters, it supplies extensive context and background information, setting the stage for the chapters to come. In general, Katarzyna Janiszewska does an excellent job of explaining how her in-depth results fit into the bigger picture and why they are significant.

# Chapter 1: Skeletal ontogeny in basal scleractinian micrabaciid corals (published in *Journal of Morphology*, 2013)

The first chapter deals with the insertion of septa in micrabaciid corals during ontogeny using a modern approach to age-old question. It develops a new model for the skeletal ontogeny based on fossil and Recent specimens in different growth stages. Using cutting-edge microscopy (serial micro-CT and SEM micrographs), higher cycle septa are not observed to form by "septal bifurcation" (the traditional model involving division of pre-existing septa) but instead they originate independently from other septa as "blades" that extend from the outermost margin of the corallite. The wall is not synapticulothecate, as previously interpreted, but is formed by pillars of invaginated wall that grow simultaneously in structural continuity with the septa. These observations are novel, and confirm the basal position of micrabaciid corals in scleractinian phylogeny, recently discovered using microstructural and molecular data. For the first time, clear differences in wall structure are shown between micrabaciids and other scleractinians, including the suborder Fungiina in which they were previously grouped. The morphologic descriptions are excellent (detailed, accurate, carefully interpreted), and reveal a deep understanding of the growth process of many different skeletal components as well as a thorough knowledge of the literature, both classical and modern. The figures are superb (including both photos and drawings), and the writing is clear, succinct, and carefully crafted. The observations are used to construct an emended diagnosis, and thus have important taxonomic implications for the group.

### Chapter 2: A unique skeletal microstructure of the deep-sea micrabaciid scleractinian corals (published in *Journal of Morphology*, 2011)

The second chapter describes two microstructural components (rapid accretion deposits [RAD] and thickening deposits [TD]) in the four known extant genera of micrabaciid corals for the first time using an array of different state-of-the-art microscopic methods (TLM, SEM, FESEM, TEM, AFM etc). It delves more deeply into the biomineralization process and thereby builds upon earlier work by Jarek Stolarski on different taxa. Katarzyna Janiszewska makes comparisons between the four micrabaciids and two common scleractinian genera, *Acropora* 

(zooxanthellate) and *Desmophyllum* (azooxanthellate), among others, and concludes that the TD of micrabaciids are unique in that they are composed of short, thin fibers that are organized in chip-shaped bundles (an apomorphy). The unusual TD conform with molecular results placing microbaciids in a separate clade that is basal to all other scleractinians (except Gardineriidae). These findings are new, and pave the way for a broader survey of similar microstructural characters across all scleractinians, which could potentially lead to the discovery of synapomorphies that are diagnostic of family- to suborder-level molecular clades. They also point to a diversity of organic-matrix mediated biomineralization strategies within Scleractinia, and indicate that biological control is not easily perturbed by environmental factors. The results contrast with those of other researchers who advocate stronger influence for environmental control, and therefore contribute to a controversial hot topic. Ongoing research is aimed at finding a common biochemical characteristic that may be responsible for the unusual TD. The figures are exceptional, and so are their interpretations.

# **Chapter 3: Biomineralization of micrabaciid scleractinian corals in the Cretaceous "calcite sea" (to be submitted soon)**

Chapter 3 examines the geochemistry of micrabaciid mineralization and biological-vsenvironmental mediation in more detail, and compares calcium carbonate in Cretaceous, Neogene, and modern specimens. During the Cretaceous, the oceans were "calcitic", whereas during the Neogene and today, they are "aragonitic". Skeletal chemistry should differ between calcitic and aragonitic seas if under environmental control. The geochemical methods used to study this question are many and state-of-the-art. They are rigorous, and include transmitted light microscopy, SEM/FESEM, cathodluminescence, NanoSIMS, Raman analysis, synchrotron XRF, and wavelength dispersive spectroscopy. Once again the research is very high in quality with exquisite attention to detail, and the figures are excellent. The results show that Mg/Ca and Sr/Ca molar ratios are similar in Cretaceous and modern specimens, even though the Cretaceous *Micrabacia* is diagenically altered from aragonite to calcite. They indicate a stable mineralogy for *Micrabacia* and support strong biological control. Furthermore, differences between Cretaceous *Coelosmilia* and *Micrabacia* may be explained by differences in organic molecules in the biomineralizing milieu, and point to a taxon-specific response, which has significant implications for scleractinian systematics.

### Chapter 4: Microstructural disparity between basal micrabaciids and Other Scleractinia: new evidence from Neogene *Stephanophyllia* (in review for *Lethaia*)

The fourth chapter uses transmitted light microscopy, SEM (including backscattered), Raman microscopy, cathodoluminescence, and XRF to examine thickening deposits in well-preserved Neogene micrabaciid *Stephanophyllia*, and finds that they consist of long and thin parallel fibers that form layers of thatch-like structures. This pattern differs from other scleractinians, including other micrabaciids, suggesting that mechanisms of biomineralization within micrabaciids are unusually diverse. Although micrabaciids first appear during the Cretaceous, the unexpected high diversity in the microstructure of the thickening deposits indicates that they may have been a primitive group that first evolved skeletons or migrated from deep water during the Cretaceous. These observations are new, and provide unique and important insight into scleractinian evolution. Once again in this chapter, the figures are elegant, and so are their interpretations.

#### Overall evaluation of the dissertation

In general, Katarzyna Janiszewska's dissertation addresses much-debated topics ("hot topics") in scleractinian evolution, specifically the mineralogy and microstructure of a poorly known basal group, the micrabaciids. Much of the work is already published by Janiszewska and colleagues, and thus has been deemed acceptable by mainstream journals in morphology and paleontology with moderate impact factors. The publications should attract the attention of a broad audience of researchers studying biomineralization and skeletal morphology in marine invertebrates. The dissertation uses state-of-the-art microscopic technology, involving careful, intricate work that requires accuracy, precision, and close attention to detail. The observations are new and original, and the interpretations are carefully reasoned and sound. The figures are exceptional. The dissertation is well-written (polished), although originally there were a few English grammatical errors which I have corrected in earlier versions of the chapters. The references are state-of the-

art and comprehensive, and reveal a clear understanding of both the classic literature and ongoing controversies. My overall impression is extremely positive, and I have no negative points. The four chapters represent unique and important contributions to the natural sciences.

#### Conclusion

The dissertation of Katarzyna Janiszewska fulfills the necessary criteria to obtain a doctoral degree (PhD). My review is positive, and I conclude that the K. Janiszewska, M.Sc. should be admitted to further steps in the Ph.D. defense procedure.

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Ann F. Budd, F. Wendell Miller Professor of Earth & Environmental Sciences Iowa City, September 19, 2014