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Biological and molecular control of calcium carbonate deposition during eggshell mineralization

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The avian eggshell is a protective, porous bioceramic that regulates the exchange of metabolic gases and water, and serves as a calcium reservoir for the developing embryo. Its formation is also the fastest calcifying process known in biology, and it occurs at body temperature and without resident cells. Eggshell calcification is an important example of a tightly controlled biological calcium carbonate precipitation process. Mineralization of the eggshell is dynamic, and the first stages of calcification occur with transient formation of amorphous calcium carbonate (ACC) mineral that possesses calcitic short-range order, which progressively transforms directly into calcite crystals without any intermediate phase. The transient ACC mineral deposits, as well as the calcite crystals derived from them, form by the ordered aggregation of nanoparticles that support the rapid mineralization of the eggshell, and explain the unique characteristics of eggshell mineral structure. The soluble precursors of the eggshell matrix are present in the acellular uterine fluid, from which they become incorporated into the calcifying shell. This organic matrix plays a key role in the nucleation and stabilization of calcium carbonate on specific sites on the eggshell membranes, determining polymorphic phase selection, and regulating crystal morphology and growth rate. Transcriptomic and proteomic studies have identified a wealth of protein matrix candidates that may regulate mineralization; we hypothesize that the most abundant and specific eggshell constituents comprise the toolkit regulating eggshell mineralization.

We will review the mechanisms regulating the precipitation of calcium carbonate and the structural organization of the eggshell and its constituent crystals from the nano- to the micrometer scale. Moreover, we will provide an overview of candidate regulatory eggshell molecules derived from comparative studies in multiple avian species, proteomics analysis of uterine fluid and eggshell composition during temporal windows in mineralization, and *in vitro* recapitulation of eggshell mineralization using purified or recombinant matrix proteins.