Supplemental 1: Background

Geologic Setting

This work results from observations made throughout the upper part of the global Katian Stage, specifically the North American Cincinnatian Series (Fig. 1; Brett et al., 2018, 2020). We have examined hundreds of thin sections made from mostly carbonate interbeds (Dattilo et al., 2019), and a few siliciclastic-rich beds throughout the Cincinnatian Series. These thin sections represent the range of carbonate environments from peritidal through offshore facies, and from relatively condensed through rapidly deposited beds (Brett et al., 2020). In nearly all occurrences of echinoderm ossicles, some consistent preservational patterns emerge. Phosphatization of echinoderm ossicles is stratigraphically nearly ubiquitous. We extrapolate from previous work (Dattilo et al., 2016, 2019) that over a thousand distinct beds throughout the succession contain detectable numbers of phosphatized ossicles. Additionally, where phosphatized ossicles occur, unphosphatized ossicles also occur, even when phosphatized ossicles are extremely abundant. In beds that are noticeable in their concentrations of phosphatic micro-steinkerns, the degree or character of the level of phosphatization is variably high or extreme. Thus, phosphatization always occurs along with at least one of two or more taphonomic styles of preservation of ossicles. We have explored a handful of these steinkern-rich occurrences (Fig. 1; Supplementary File 2, Fig. S2-1) more thoroughly, and we illustrate ossicles found in three of these samples in this paper.

The sequence stratigraphy of the Cincinnatian Series was recently revised by Brett et al. (2020).

Sedimentology of Cincinnatian Shell Beds

Early work on the distinctive mixed carbonate/siliciclastic beds of the Cincinnatian hypothesized that the carbonate shell beds, often so obviously reworked, formed during shallow water periods when the seafloor was above storm wave base, whereas the muddy shale beds were deposited in deeper water when the seafloor was below storm wave base (e.g., Jennette and Pryor, 1993).This hypothesis was falsified based on subsequent observations. In this shallow epeiric sea, significant sea level changes at the meter scale would be required to move the seafloor from wave base to below, and these changes would equal or exceed changes in water depth found at much larger scale cyclicity (Brett et al., 2020). The mud intervals include many beds with evidence of very rapid deposition as obrution deposits, whereas the carbonate intervals are often amalgamated, with evidence of mixed taphonomies indicating slow accumulation and condensation (Brett et al., 2008). Deeper water faunas are preserved in grainstones, rather than shale, and both carbonates and shales show evidence of disruption by storms (Dattilo et al., 2008). Tracked from proximal through distal areas of the depositional basin, the distribution of these two facies supports the interpretation of the carbonate grainstones as having accumulated slowly in deeper water, and the shales as representing more rapid deposition in shallower water (Dattilo et al., 2012)

Deposition of Phosphatic Cincinnatian Microsteinkerns

The deposition of sediment rich in phosphatic grains has long been associated with sea level changes (Kazakov, 1937). One well known hypothesis is that “phosphogenesis” occurs when sea level is high, potentially in tandem with upwelling of nutrient-rich deep water onto continental shelves, and then “phosphate deposition” occurs when sea level falls and the products of phosphogenesis are concentrated due to a higher energy sedimentological regime (Baturin, 1971; Mullins and Rasch, 1985; Föllmi, 1990, 1996).

The sedimentology of the Cincinnati shell beds is inconsistent with the classic two-phase phosphogenesis-phosphate deposition model because Cincinnatian limestones definitely did not form during shallowing periods, but more likely formed during deepening periods (Brett et al., 2008; Dattilo et al., 2008; Dattilo et al., 2012). The PPC model (Freeman et al. 2019) integrates previous understanding of the phosphogenesis and phosphate deposition with the condensation-based models of shell bed formation that were developed for Cincinnatian strata. In this model phosphate is formed and concentrated by repeated storms acting on seafloor accumulations of shells exposed for variable periods of condensation.

SSF-style preservation is facies-dependent (Jacquet et al., 2019) and associated with mild to extreme stratigraphic condensation (Dattilo et al., 2019; Freeman et al., 2019). This particular type of CFA mineralization and subsequent phosphatic sediment deposition is the result of a geochemical process that operates in episodically disturbed sediments during periods of slow or no net sedimentation (Freeman et al., 2019). Infrequent but repeated high-energy events result in repeated cycles of phosphate precipitation. When a small shell is buried initially, if buried as a live organism, soft tissue decay will form a center of reduction. Each of these is surrounded by an oxidative gradient and this gradient powers the “iron-pumping mechanism” whereby phosphorus is removed into solution from iron oxyhydroxides, then, as oxygen increases, is transferred to carbonate fluorapatite (CFA) (e.g., Berner, 1973; Shaffer, 1986; Froelich, 1988; Ingall and Jahnke, 1997). As decay proceeds and organic fuel is consumed, the reductive halo around the shell decreases in size, sweeping stripped phosphorus from the surrounding sediments and concentrating it in the small cavity of the shell. The CFA that results from this process forms nucleation sites for subsequent CFA mineralization as the shell continues to be entrained in multiple cycles, adding small amounts of CFA with each reworking and reburial event through the polycyclic phosphogenic condensation (PPC) model (Dattilo et al., 2019; Freeman et al., 2019).

The phosphatization process typically results in the formation of microsteinkerns which are internal molds, typically approximately 0.5 millimeters in diameter. Phosphatization is far from complete within that half millimeter of pore space. Most microsteinkerns of larger chambers, such as gastropods and bivalves, also contain significant infiltrated sediment (siliciclastic or carbonate particles) of roughly silt size (4-63 μm) within the pore space, which results in 10 μm scale sub-porosity within the cavity. The precipitated CFA effectively cements the particles together, resulting in a durable solid microsteinkern. Without the sediment infiltration, phosphate could only nucleate on the walls of the original shell material, which would result in a fragile, hollow microsteinkern that would easily disintegrate. The nucleation of CFA on the surface of sediment particles increases the surface area upon which CFA can nucleate during successive phosphogenesis, enhancing the process (Föllmi, 1996; Galfati et al., 2010).

One prediction of the PPC model is that longer periods of sediment starvation will lead to both more mature sediments and a higher concentration of SSF-style microfossils. Dattilo et al. (2019) tested this prediction through analysis of Cincinnatian carbonates in thin section and demonstrated that textural maturity and shell fragmentation correlate positively with the abundance of phosphatic steinkerns.

Lamboy Process, Grain Maturity

The same model predicts that phosphatic grains would not only proliferate and be concentrated with time, but that individual grains would become progressively more phosphatic as they are cycled through repeated phosphogenic phases of bed development. Grains become more diagenetically mature with greater residence time in the taphonomically active zone on the seafloor.

Lamboy (1982, 1987) observed a maturity succession of phosphatized echinoderm ossicles from Cenozoic phosphorites of Northern Africa. This succession fits the predictions of the PPC model. In the first stage of Lamboy (1987) grain maturity, internal phosphatic coatings progressively occlude μm-scale stereomic spaces, leaving the original calcitic skeleton intact. Subsequently the original calcite dissolves and the resulting space is then also occluded by progressive phosphatic coatings.

Lamboy (1987) undertook an extensive study of phosphatized Cretaceous echinoderm ossicles from Guinea Bissau, which led to a hypothesis of a succession of diagenetic stages in the phosphatization of an echinoderm ossicle. He concluded that the phosphatization process began with CFA filling the interstices of the echinoderm stereom ("Lamboy process 1"; Fig. 1(C)). As these coatings are accreted layer by layer, they eventually occlude the stereomic space entirely. Subsequently, as a second step, the original trabecular calcite may dissolve and the vacated spaces may then fill with newly formed diagenetic phosphate ("Lamboy process 2"; Fig 1(F)). This version of replacement is also a kind of molding with the original skeleton dissolved and the replacement material making a mold of the resulting cavity, resulting in a cast. Ultimately this preservation process depends on a slow and intermittent minute dissolution-then-replacement cycle that is repeated to preserve some remnant or ghost of the original hard part. In fact, in the true Lamboy (1987) process-style replacement, the quality of the replacement is a matter of scale. Our study tests the Lamboy hypothesis that initial phosphatization of echinoderms is in the form of calcium fluorapatite micromolds of intraskeletal space. These steps may in fact occur in other small shells that have been previously occluded with phosphate (Dattilo et al., 2016) but would be much more difficult to detect due to the infiltration of sediment after death.

SSF-style Preservation Through Geologic Time

Phosphatic microfossils are well known as the Early-Middle Cambrian small shelly fauna (SSF) (e.g., Matthews and Missarzhevsky, 1975) but are not temporally limited (i.e., Dzik, 1994; Freeman et al., 2019). Evidence of the potentially cyclic nature of phosphate mineralization that leads to SSF-style preservation (Dattilo et al., 2019; Freeman et al., 2019) may be more easily observable in echinoderm ossicles because their micron-scale porous, complex internal structure excludes infiltration of sediments, creating a natural “reaction chamber” for diagenetic mineral deposition. As a case study for phosphatic ossicle preservation, we investigate the mineralization and taphonomic pathways for one such post-Cambrian occurrence.

Echinoderm ossicles and other phosphatized microfossils occur as minor constituents (<1% to 10%) in thousands of centimeter-scale subtidal shell-bed limestones throughout the 300 meters of Upper Ordovician (Katian) strata in the Cincinnati, Ohio region ("Cincinnatian strata") (Dattilo et al., 2016). In only a few strata, apparently significantly associated with larger scale (3rd order) sequence surfaces (basal TST and MSS), are they sufficiently concentrated to be observable in the field (Brett et al., 2018; Brett et al., 2020).

Insights into the preservation of Cincinnatian SSFs may apply to SSF-style preservation generally. The sedimentology and paleontology of these deposits are well constrained, which informs interpretation of the SSFs found therein. Based on sedimentological models for Cincinnatian strata that involve condensation with iterative disturbance (Brett et al., 2008; Dattilo et al., 2008; Dattilo et al., 2012). Freeman et al., (2019) proposed a compatible model to explain SSF-style preservation. The polycyclic phosphogenic condensation (PPC) model explains SSFs as a result of small shells residing for long periods of time in the taphonomically active zone, and exposed to occasional reworking events.

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