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Benjamin F. Dattilo  
*Indiana University - Purdue University Fort Wayne, dattilob@ipfw.edu*

Rebecca L. Freeman  
*University of Kentucky, rebecca.freeman@uky.edu*

Winfried S. Peters  
*Indiana University - Purdue University Fort Wayne, petersw@ipfw.edu*

William P. Heimbrock

Bradley Deline  
*University of West Georgia*

*See next page for additional authors*

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GIANTS AMONG MICROMORPHS: WERE CINCINNATIAN (ORDOVICIAN, KATIAN) SMALL SHELLY PHOSPHATIC FAUNAS DWARFED?

BENJAMIN F. DATTILO,¹* REBECCA L. FREEMAN,² WINFRIED S. PETERS,³ WILLIAM P. HEIMBROCK,⁴ BRADLEY DELINE,⁵ ANTHONY J. MARTIN,⁶ JACK W. KALLMEYER,⁷ JESSIE REEDER,¹ and ANNE ARGAST¹

¹Department of Geosciences, Indiana University−Purdue University Fort Wayne, 2101 East Coliseum Boulevard, Fort Wayne, IN 46805-1499, USA, dattilob@ipfw.edu, reedjl02@students.ipfw.edu, argast@ipfw.edu; ²Department of Earth and Environmental Science, University of Kentucky, Lexington, KY 40506, USA, rebecca.freeman@uky.edu; ³Department of Biology, Indiana University−Purdue University Fort Wayne, 2101 East Coliseum Boulevard, Fort Wayne, IN 46805-1499, USA, petersw@ipfw.edu; ⁴Dry Dredgers, 1621 Westwood Avenue, Cincinnati, OH 45214, USA, billheim@cinci.rr.com; ⁵Department of Geosciences, University of West Georgia, Carrollton, GA 30118, USA, bdeline@westga.edu; ⁶Department of Environmental Sciences, Emory University, Atlanta, GA 30322, USA, geoam@emory.edu; ⁷Dry Dredgers, 4663 Moselle Drive, Liberty Township, OH 45011, USA, paleojack@fuse.net

*Corresponding author

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ABSTRACT: Small fossils are preserved as phosphatic (carbonate fluorapatite) microsteinkerns (~0.5 mm diameter) in Upper Ordovician beds of the Cincinnati area. Mollusks are common, along with bryozoan zooecia, echinoderm ossicles, and other taxa. Similar occurrences of Ordovician micromorphic mollusks have been interpreted as ecologically dwarfed and adapted to oxygen-starved conditions, an interpretation with implications for ocean anoxia. An alternative explanation for small phosphatic steinkerns is taphonomic. Stable carbonate fluorapatite selectively filled small voids, thus preserving small fossils, including larval/young mollusks. Reworking concentrated small phosphatic steinkerns from multiple generations while larger, unfilled calcareous shells were destroyed, resulting in small fossils progressively replacing larger fossils. With thin sections and insoluble residues, we document evidence that many of these steinkerns are incomplete (“teilsteinkerns”) recording small parts of larger, normal-sized animals, or juveniles, along with smaller species. This finding suggests that these fossil assemblages are taphonomically, not ecologically, size-limited. Based on the ecology of modern oxygen minimum zones in which shelled mollusks are rare, the presence of abundant shelled organisms actually argues against severe oxygen stress. Our results also imply that the process by which the “small shelly fossils” of the Cambrian were preserved continued into the Ordovician.

INTRODUCTION

Abundant minute phosphatic steinkerns of gastropods (assigned to the genus *Cyclora* Hall 1845) and other organisms have been long-documented in certain shell beds and phosphorites of the Upper Ordovician around Cincinnati (Hall, 1845; Meek, 1873; Ulrich, 1879; S. Miller, 1874, 1882; A. Miller, 1896; Foerste, 1913; McFarlan, 1931; Holland, 1993; and McLaughlin et al., 2008). Collectively these assemblages are known locally as the “*Cyclora*
fauna”. Recent detailed examinations of the Cyclopa fauna are few (e.g. Martin and Pope, 1985, Martin, 1986), but taxonomic composition and taphonomy suggest that Cincinnati Cyclopa assemblages are similar to coeval assemblages of diminutive phosphatic steinkerns in the Maquoketa Formation of Iowa (Vendrasco et al., 2013). The Iowa assemblages have been taken as evidence for “dwarfed” or “depauperate” faunas adapted to an oxygen-stressed environment, related to the invasion of cold, oxygen-poor and phosphate-saturated water masses from the deep ocean (Ladd, 1929; Snyder and Bretsky, 1971; Frest et al., 1997; Witzke and Heathcote, 1997; McLaughlin et al., 2011; Johnson, 2013). This interpretation has profound paleoceanographic and paleoclimatic implications. A correct interpretation of these fossils is crucial in the context of the debate over the timing and effect of Late Ordovician climate change and glaciation (e.g. Brenchley et al., 1994; Brenchley et al., 2003), with Cincinnatian phosphates interpreted as evidence of cold oceanic water masses invading the Laurentian epeiric sea long before the end-Ordovician event (Saltzman and Young, 2005; Holmden et al., 2013) even as geochemical evidence against cooling mounts (Quinton and MacLeod, 2014; Hughes et al., 2015).

The fact that these micromorphs are consistently preserved as phosphatic steinkerns suggests an alternative hypothesis, that this mode of preservation is biased toward the preservation of small fossils. With this in mind, we sampled the Cyclopa fauna from various horizons of the Cincinnatian succession and examined them for evidence of dwarfism and size-biased taphonomic process. Our observations suggest that the assemblages result from selective preservation of juvenile and small individuals, and smaller parts of larger sized individuals, all within a community exhibiting the normal range of sizes for Cincinnatian taxa. This bias results from the pore-size filling limitations of the phosphogenic process and the relative durability of calcium fluorapatite with respect to calcite or aragonite over long periods of seafloor exposure or
reworking. In the presence of terrigenous influx (e.g. erosion of igneous rocks from the Taconic Orogen) unusual chemical, oceanic, or climatic conditions may be unnecessary to explain these assemblages.

BACKGROUND: ECOLOGY OR TAPHONOMY?

The origin of these assemblages, and their relationship to the larger, more “normal” and abundant fossils of the Cincinnatian Series have been debated for decades. Some authors concluded that they were diminutive adults (Hall, 1845; Miller, 1882), while others interpreted them as protoconchs (Knight et al., 1960; Grabau and Shimer, 1909; McFarlan, 1931; Martin and Pope, 1985; Martin, 1986; Holland, 1993) or juveniles (Cumings, 1907) of typical Cincinnatian gastropods.

To establish that these are diminutive adults (as suggested, for example, by Snyder and Bretsky, 1971 and Witzke and Heathcote, 1997) would require establishing that they had in fact reached full maturity at a smaller size than normal (Tasch, 1953; Hallam, 1965). The alternative hypothesis, that the process of creating these steinkerns was biased toward smaller sizes, has not been invoked to explain the Cyclora fauna. However, a similar taphonomic model has been used to explain the widespread occurrence of small pyritized ammonites in Jurassic and Cretaceous shales (Hudson and Palframan, 1969; Marcinowski, 1980; Hudson, 1982; Fisher 1986; Kennedy, 2004). This inference runs counter to the repeated observations that smaller shells are more rapidly destroyed in sedimentary environments (e.g. Cummins et al., 1986; Kidwell and Bosence, 1991; Cooper et al., 2006; Kosnik et al., 2007). However, calcium fluorapatite (CFA) is more durable than calcite (e.g. Baturin, 1971; Glenn and Arthur, 1990; Glenn et al., 1994;
Föllmi, 1996; Trappe, 1998), so once formed, these small steinkerns would outlast much larger calcitic shells.

STRATIGRAPHY AND LOCALITIES

All of the specimens were collected from the Cincinnatian (Katian, Ordovician) outcrops in the Tri-state area around Cincinnati, Ohio (Fig. 1). Collections ranged in stratigraphic position from the Maysvillian Fairview Formation to the Richmondian Liberty Formation (Fig. 2). To clarify relative stratigraphic position, we list Cincinnati equivalents (Caster et al., 1955) for local stratigraphic names. Samples in this study are from the following localities; they are listed in stratigraphic order from lowest to highest:

A. The phosphatic zone in the Fairmount Member of the Fairview Formation at a large cut on Indiana 48 near the intersection with US 50 in Lawrenceburg, Indiana (LBG 36.5).
39.099008°N, 84.877145°W

B. A phosphate-poor molluscan packstone in the upper Fairview Formation below the Miamitown Shale Member, exposed in an abandoned quarry face below a Christ Hospital parking area at the corner of Rice and Gage Streets, Cincinnati, Ohio (CHS).
39.120719°N, 84.513546°W

C. A relatively phosphate-poor *Pseudolingula* and *Rafinesquina* bed (Freeman et al., 2013) in the upper Fairview near the base of the Miamitown Shale, exposed in the spillway at Harsha Lake, Ohio (HRL). 39.030068°N, 84.157663°W

D. A thick phosphatic zone in the Fredericktown outcrop (FRD 16.6), middle Grant Lake Formation, probably Corryville Member equivalent, on US 150 near Fredericktown, KY.
37.766912°N, 85.355389°W
E. A 10 cm thick phosphate bed in the The Arnheim phosphatic zone in Florence, Kentucky exposed at the Florence Freedom Ball Park (FFP), currently known as UC Health Stadium. 38.982277°N, 84.637560°W

F. A thick phosphate-rich bed exposed at the base of the Clarksville Member of the Waynesville Formation in a US 421 road cut on the hill just south of Milton, Kentucky (MLT). 38.776673°N, 85.364136° W

G. A thin phosphate-rich bed in the Liberty Formation in the US 421 roadcut at Madison, IN (MAD 5.5). 38.776673°N, 85.364136°W

METHODS

Previous to this study, the authors had identified beds rich in non-skeletal phosphates over many years in the course of routine stratigraphic and paleontological field work. The beds are generally recognized by the presence of snail and bryozoan steinkerns visible with a hand lens. These beds were sampled previously or resampled for this study. One sample (Sample C, Harsha Lake), collected in a previous study (Freeman et al., 2013), revealed the presence of phosphatic particles only after dissolution in acetic acid.

Oriented samples, two to ten kilograms each according to bed thickness, were cut vertically for polished slabs and thin sections. As much as one kilogram of each sample was dissolved in a buffered 10% acetic acid solution. Residues were picked for phosphatic particles and other fossils, including non-skeletal internal molds (steinkerns), conodonts, and phosphatic brachiopods.

Selected areas in thin sections were imaged with photomicrographs to show non-skeletal phosphatic particles in sedimentological context. For thicker sections, photomicrographs were
made at several focal depths within the section and stacked using Zerene Stacker (http://www.zerenesystems.com/) image stacking software to create images focused through the entire thickness of the slide. Fossils from acid residues were imaged with a Hitachi S3400N scanning electron microscope, and elemental distributions of thin sections were mapped using the associated EDS.

Specimens of the northern moon snail, *Lunatia heros*, were used as modern analogues to explore gastropod micro-steinkern geometry. Artificial rubber steinkerns were made by immersing specimens in silicone rubber (Alumilite High Strength 2), which were then evacuated three times to remove air bubbles, cured overnight, and cut out of the cured silicone block using a craft knife. The internal molds were then pulled out of the shells, and the now-empty shells cut in half along the axis using a wafering saw [Buehler IsoMet 1000]. Other modern and fossil gastropods were also sliced axially.

**OBSERVATIONS**

**Gastropods**

Simplified to its basic geometry, a gastropod shell is a helically twisted cone which expands with growth (e.g. Raup, 1961, Urdy et al., 2010). Although some modern gastropods (e.g. conchs) change the pattern of expansion or thicken the shell around the aperture at a determinant size, most gastropods, including all known gastropods of the Cincinnati Ordovician, show no allometry at maturity (e.g. Cummings, 1907; McFarlan, 1931). This isometric growth pattern poses a problem for demonstrating dwarfism because the lack of a terminal allometry precludes determination that a fossil gastropod was sexually mature. Thus, for a given
micromorphic steinkern, it is impossible to distinguish a normal-sized juvenile from a dwarfed adult.

*Phosphatic steinkerns are not complete.*—Another complication of determining the maturity of gastropods is that their isometric conical expansion and helical growth predicts that a small individual is similar to the apex of a large individual. Therefore, a partial fossil of a larger gastropod, one that only records the apex, might be interpreted as the remains of a smaller gastropod. Some record of the apertural lip (visible even without thickening), not merely a fractured edge, is necessary to determine the size of a fossil gastropod (Hallam, 1965). If the phosphatic gastropod steinkerns of the *Cyclora* assemblages correctly record the full size of the original shells, then some evidence of the apertural lip should be apparent on specimens (Fig. 3).

We examined hundreds of gastropod steinkerns from residues looking for imprints of unbroken apertures. We found no imprints of apertures, neither broken nor unbroken. Most steinkerns were broken off distally, and some specimens displayed a smooth meniscus-like distal termination (Fig. 4), where the end of the steinkern forms a concave curved surface as if it were a liquid adhering to the shell interior. In either case, the full size of the gastropods, which should have been marked by an apertural imprint or end of shell, was not preserved. Although the meniscus-like termination could be the mold of an operculum, in some cases it was seen on both ends of an incomplete steinkern (a “teilsteinkern”, new term), or only on the smaller end of a teilsteinkern (Figs. 4E–H). Another possible cause for the meniscus-like impression is a smaller gastropod or bivalve embedded somewhere within the spiral tube. We observed this relationship in some gastropod molds. Removal of the smaller steinkern from the aperture would result in a smooth meniscus-like impression in the larger steinkern.
However, similar meniscus-like features can be seen in cross-section in thin sections (e.g., Figs. 4A, B), in a position clearly further within the interior of the shell than would be expected if it recorded the impression of the operculum, and generally without any sign of having been formed by embedded fossils. A search of thin sections revealed several examples of small gastropods with shell remnants preserved, which were only partially filled with phosphate. This suggests that the meniscus was not a molded surface, but the depositional limit of phosphate that was not able to fill the entire cavity. Therefore, we concluded that phosphatic steinkerns are typically teilsteinkerns, appearing smaller than the gastropods that they record, making it impossible to gauge the size of the original shells from the dimensions of the teilsteinkern.

*The gastropod apex is occluded as the animal grows.*—The incomplete nature of the teilsteinkerns prevents direct determination of the original size of the gastropods, but among the variety of micro-steinkern *Cyclora* species differentiated, for example, by apical angle (e.g. Cumings, 1907), the variation might better be attributed to ontogeny. Specifically, steinkerns of varying shapes display the same spectrum from tightly coiled forms with bulbous protoconchs to loosely coiled forms with detached whorls and sharp proximal tips. We hypothesized that the internal geometries (recorded by internal molds of the shell cavity) of gastropods might be altered significantly with ontogeny, thus departing from the simple isometric spiral shape that characterizes the external shell. This variation could be used to determine the relative age, and therefore relative size, of conspecific teilsteinkerns.

We examined a variety of modern gastropods, both in growth series and in axial section to determine how the shell thickness and internal space of the apical whors change with age. Larval shells start thin, and more mature shells contain thicker internal deposits in the apical whors. The functional role of this thickening is readily apparent; if the protoconch were left in
its original thin-shelled state, it would break easily during minor collisions given the increased
inertial mass and muscle strength of the larger animal. This damage would expose the animal
with potentially fatal consequences. Axial sections of two sizes of the northern moon snail,
*Lunatia heros* (Fig. 5) illustrate how shells are thickened progressively from the inside, resulting
in the occlusion of earlier whorls. Similar thickening was observed in every gastropod species
that we examined, including three different species from the Ordovician of the Cincinnati area.
Sectioned Ordovician gastropods (Fig. 6) include high spired *Paupospira bowdeni* (Safford,
1869; Fig. 6A–B) and low spired *Clathrospira conica* (Ulrich & Scofield, 1897; Fig. 6C–D)
gastropods from the Marble Hill Bed (Waynesville Formation, Clarksville Member) near
Bedford, Kentucky (Swadley, 1979), where aragonitic shell structure is faithfully recorded in
recrystallized calcite (Harrison et al. 2010); Sectioned specimens of *Cyclonema* (possibly more
than one species; e.g. Fig. 6E–F), which have originally calcitic outer shells and recrystallized
aragonitic inner deposits, showed the pattern as well. Apical wall thickening and occlusion
appears to be a common process of gastropod ontogeny.

Internal shell remodeling by gastropods is well documented, and processes include
reducing shell mass by internal dissolution of older whorls (Kohn et al., 1979; Solem, 1983),
dissolving the penultimate whorl from the outside (Signor, 1982), or sealing off and shedding the
apical portion of the shell altogether (decollation; Gittenberger and Povel, 1995). Furthermore,
many mollusks are known to deposit additional material such as nacre on the inner surfaces of
their shells, and the underlying molecular mechanisms are increasingly well understood (e.g.
Nudelman et al., 2008; Furuhashi et al., 2009). Nevertheless, we could find no previous studies
addressing the progressive filling of apical whorls through ontogeny.
This process has a profound effect on the shapes of small gastropod teilsteinkerns, and allows them to be arranged in a growth series (Fig. 7), even though teilsteinkerns do not record any direct evidence of the size of the original shell. In fact, some of the steinkerns from smaller shells are larger than the steinkerns from larger shells. Steinkerns that show a bulbous protoconch mold (e.g. Frýda, 2012) are younger, whereas those that terminate proximally in a point represent more mature shells. Therefore, the original relative size might be surmised from apical steinkern shapes (Fig. 8). This observation suggests that there is a limit to the size of the original shell that can be represented by such a small steinkern, because the first small whorls will eventually be occluded entirely, leaving no space for a steinkern to fill. The Cyclora steinkerns thus represent a mixture of larval and juvenile shells at various stages of growth, possibly with some diminutive adult forms with proportionally small apical occlusion. The juveniles were originally larger than any of their preserved steinkerns, but centimeter-scale individuals, more typically preserved as carbonate-mud steinkerns, are not represented among these phosphate teilsteinkerns of the shell cavity.

Umbilical steinkerns record the presence of larger gastropods.—In addition to the shell cavity discussed above, many gastropods have an umbilical cavity in which an internal mold can form (Fig. 3). Umbilical steinkerns are less well known and less well studied than shell-cavity steinkerns, but our initial investigations suggest that they are quite commonly preserved in the macro-fossil record (Fig. 9). For the purposes of teasing out taphonomic size selectivity and ecological dwarfism, these steinkerns are useful because, to a first approximation depending on precise shell geometries, gastropod umbilical cavities range from a fifth to a tenth of the diameter of the corresponding whorl of the shell cavity (Fig. 9H). Thin sections (Figs. 9A-C) and acid residues (Figs. 9D, J–N) contain many umbilical steinkerns that are still associated with their
shell cavity steinkerns. They also occur in isolation (Figs. 9E–G). The largest of these isolated steinkerns (Figs. 9G, F) are similar in cross sectional diameter to the typical-sized *Cyclora* shell cavity steinkern (0.2 – 0.7 mm), but they represent snails five to ten times larger. These larger snails are preserved only as umbilical steinkerns with no corresponding shell cavity steinkern.

**Monoplacophorans**

Mixed among the gastropods of most residues are the planispiral shells of monoplacophorans (Fig. 10). Some are distinctive enough to be provisionally assigned to the genus *Cyrtolites* (Figs. 10A–C), which is well represented in the Cincinnatian macrofauna (Wahlman, 1992). The steinkerns of monoplacophorans are similar to those of gastropods in that they commonly have a meniscate distal termination and do not completely fill the shells in thin section (Figs. 10A, B). In residues they commonly include a pair of umbilical steinkerns which record more (but not all) of the original shell size than do the associated shell cavity steinkerns (Figs. 10C, D; absent in Fig. 10E). These monoplacophorans differ from gastropods in that they show no sign of apical occlusion (Fig. 10B). This probably is a consequence of the fact that the apex of planispiral shells is not exposed to breakage hazards like that of helically spiraled shells. Without this apical thickening, we were unable to reconstruct, estimate, or guess the original shell size from incomplete teilsteinkerns; a millimeter-sized steinkern could represent a centimeter- (Fig. 10A “normal”) or millimeter-sized (Fig. 10B “diminutive”) original.

**Bivalves**

Whole bivalves, generally less abundant than gastropods, are preserved as steinkerns less than about 0.5 mm in minimum dimension (Figs. 11A–E). These, along with gastropods, serve as the basis for interpreting phosphatic steinkern assemblages as diminutive faunas. Unlike the steinkerns of gastropods or monoplacophorans, these steinkerns filled the entire enclosed space
between the two valves of the shell, so there is no question that they represent the full size of the original. Whether these clams were small species, juveniles of larger clams, or dwarfed individuals is an open question (requiring careful taxonomy), but they were certainly diminutive.

Larger articulated bivalves lack narrow interior spaces and apparently did not form phosphatic steinkerns, but disarticulation exposes hinge teeth. A problematic phosphatic fossil commonly found in residues (Figs. 11F, G) proves to be the molds of the spaces between teeth of *Lyrodesma*, a small (~1 to 2 cm), but not diminutive clam (Figs. 11H, I). These “steinkerns” show the unique structure of *Lyrodesma* teeth and can be characterized as uniformly thin “plates” with curved concentric ridges and grooves on either side. They sometimes occur as “clusters” (Figs. 11J, K) that record the original arrangement of teeth in the clam. The plates incorporate whole phosphatic bivalve (Figs. 11A–E), gastropod, and other steinkerns small enough to fit within (Fig. 11L), illustrating their origin as fillings, or hinge tooth molds. The average size of *Lyrodesma* hinge tooth molds from the Florence, Kentucky site (Fig. 1, FFP, site E) is 1.6 mm (n = 105, 0.95 confidence = 0.0698). We were able to measure the hinge-tooth and shell length (hinge to valve edge) of six valves of complete, non-phosphatized *Lyrodesma* ranging from 9 to 16 mm in length, and obtained an average valve length to hinge-tooth length ratio of 7.14. These measurements suggest average valve lengths for the phosphatic valves of 11.4 mm, well within the normal size range for *Lyrodesma*. The valves were collected from the Kope Formation, and may represent a different species than the Florence *Lyrodesma*, and size ratios could be variable with ontogeny, therefore a more precise determination of size is not possible. However, these inter-hinge-tooth molds demonstrate that macroscopic bivalves were present in the original community now represented in the fossil record by a preponderance of tiny steinkerns.
Much of the literature of phosphatic microfossils concentrates on the gastropods and bivalves. In picking residues, we found that samples varied in their relative abundances of taxa. Gastropods and bivalves may be relatively rare in phosphatic residues, while echinoderm ossicles (Figs. 12A–F) or bryozoan zoöcial molds (Figs. 12G–L) are common or abundant. Brachiopods, trilobites and other fossils (Fig. 13) are also found as partial molds, either of smaller interior pore spaces, or of small patches of external surfaces.

**Echinoderms.**—Echinoderm ossicles (Figs. 12A–F), which originally appeared to be replaced by phosphate, are in reality internal molds of the stereom. The relationship is clearly evident in thin section (Figs. 12A, B), where both the original calcitic skeleton and phosphatic mold are preserved. Effectively each ossicle is a single complex millimeter-scale pore consisting of a network of simple interconnected 10-micron-scale pores that permeate a latticework of rods of high Mg calcite. Thus, their preservation is only subtly different from the preservation of other phosphatic steinkerns that filled simple millimeter-scale pores that were filled in life by stromal tissue. Even this difference may be superficial, as the phosphate steinkerns of gastropods (and others) are not pure, but generally include silt-sized grains of quartz and other siliciclastics that render the open space of the shell interior a network of even smaller, yet connected spaces.

Determining whether the echinoderm assemblage is dwarfed or taphonomically biased is difficult for several reasons. First, the ossicles are parts of a multi-element skeleton such that there is less of a correlation between the size of the ossicle and the size of the individual. Many Cincinnatian camerates (e.g. *Xenocrinus*) could grow to 30 cm tall and disparids (e.g. *Cincinnaticrinus*) can reach lengths of over a meter (Warn and Strimple, 1977, Brett et al., 2008). However, complete individuals are rare or nonexistent in most beds so it is unclear
exactly how columnal size correlates to body size. In addition, several Cincinnatian crinoids exhibit significant shifts in columnal size temporally as well as environmentally (Deline, 2009), which is likely a combination of ecophenotypy and gradual evolutionary change (e.g. the anagenetic change from *Cincinnaticrinus varibrachialus* to *C. pentagonus*). Finally, columnals disarticulate quickly following the death of the organism and, therefore, often behave as sedimentary particles that are subjected to sorting and winnowing (Meyer and Meyer, 1986).

Nevertheless, crinoid columnal size does vary across the type Cincinnatian so the ossicles from the current study can be analyzed to determine if they are diminutive in size compared to other assemblages.

The ossicles in the current study (Figs. 12A–F) are small (millimeter scale) and dominated by disarticulated columnals and rare uniserial brachials. Disarticulated columnals in the type Cincinnatian can be readily identified to genus level (Meyer et al., 2002) and this assemblage is typical for the Waynesville with abundant *Cincinnaticrinus* (Figs. 12C), and common *Xenocrinus* (Fig. 12E), as well as a rare and fragmented camerate crinoid (Fig. 12D). With the exception of *Anomalocrinus*, Cincinnatian crinoid columnals are small and the sizes of the phosphatic ossicles in the current study are comparable to their non-phosphatic counterparts from equivalent stratigraphic horizons based on museum and field observations. The *Cincinnaticrinus* columnals in the current study have an average size of 2.23 mm (SD 0.8 mm, n = 156), which is statistically indistinguishable (Wilcoxon Rank Sum Test, p = 0.13) from Richmondian calcitic assemblages (n = 57; Deline, 2006). Columns of 200 *Xenocrinus* from a 2,000 cm² deposit in the upper Waynesville/lower Liberty range from 0.5 to 1.5 mm in diameter, comparable with those recovered in samples in this study.
Although the individual ossicles are small, they are parts of larger organism. While the sizes of those larger organisms remain unknown, these normal-sized ossicles cannot be taken as evidence for dwarfism.

Bryozoans.—Bryozoans (Figs. 12G–J), mostly trepostomes, but including cryptostomes, are preserved as phosphatic internal molds of the cylindrical zooecia (Figs. 12G, H), hundreds or thousands of which make up a single colony (or zoarium). The phosphatic zooecial steinkerns range in diameter from 0.1 to 0.3 mm, normal for bryozoans. Ramose bryozoans recovered partially intact from residues (Figs. 12I) are predominantly very small colony forms, whereas other fragments (Figs. 12J, K) suggest larger colonies. The smaller colonies and fragments found in residues are explained by the extreme fragility of these fossils once dissolved from the stony skeletal walls. The interconnections are very small and weak, and cannot hold enough weight for a larger colony to stay intact. Examination of thin sections from throughout the Cincinnatian suggests that bryozoan colonies of much larger size also developed phosphatic steinkerns in their zooecia (Figs. 12G–H).

Other taxa.—A variety of other taxa are found in the “Cyclora fauna” preserved either as molds of intragranular (Figs. 13A, D, E) or intergranular porosity (Figs. 13A–C). Molds of borings in larger taxa (Fig. 13A) would appear as peloids in the sediment as the larger shell was eventually destroyed. Silt preserved between larger grains was cemented by phosphate into clumps found in residues (Figs. 13C, D) that are covered in molds, usually of smaller fossil fragments. Some of these show external and internal molds of brachiopods, such as Rafinesquina (Figs. 13B, C), recognizable as a partial external mold because of its distinctive ornament (Fig. 13C). Trilobites are recognized as internal molds of smaller distinctive parts, like hollow spine
tips, or the area beneath the doublure (Figs. 13D, E), and represent smaller to more normally sized individuals.

DISCUSSION

Taphonomy, not Ecology

The inescapable conclusion of this study is that Cincinnatian phosphogenesis was limited to filling sub-millimeter (approximately sand-sized) pore spaces, a finding consistent with previous work on many (but not all) other phosphate-rich strata (e.g. Jarvis, 1980; Odin and Letolle, 1980; Lamboy, 1982, 1987; Krajewski, 1984; Slansky, 1986; Dzik, 1994; Hendrix and Byers, 2000). The fact that complete gastropod steinkerns are not observed, and that they are commonly terminated with a meniscus-like curved surface, is strong support for partial filling of the small apex of larger snails. The cause of this meniscate morphology is subject of ongoing research (Dattilo et al. 2013; Dattilo et al. 2015a; Reeder et al. 2015), but may be related to the tendency for phosphate to form thin isopachous cements that coat surfaces. The presence of umbilical phosphatic steinkerns only (no phosphatic steinkerns of the corresponding shell-cavity) from full-sized gastropods, the obviously partial phosphatic molding of many Cyrtolites monoplacophorans, and phosphatic hinge tooth molds only (no full phosphatic steinkerns) from full-sized Lyrodesma bivalves provide further support that this assemblage includes common Cincinnatian taxa of normal size.

Thus, there is abundant evidence that at least some phosphate molds formed from a normal fauna. The various early growth stages molded in the apical parts of gastropod steinkerns suggest that many of these diminutive gastropod fossils represent juvenile or larval forms. The presence of umbilical steinkerns of larger gastropods, preserved ossicles of echinoderms, zooecia
from bryozoans, phosphate-infilled macroborings within full sized brachiopods and partial
imprints of these brachiopods suggests that normal-sized shells were present, but incompletely
molded in the same phosphatizing environment.

Ongoing investigations with acid digestion of Cincinnatian fossiliferous limestones have
revealed that almost all of them contain some (if only a very few) small phosphatic steinkerns, as
was the case with the Harsha Lake sample (Freeman et al., 2013). Thus, the Ordovician small
shelly fossils are ubiquitous in the richly fossiliferous and diverse shell bed deposits of the
Cincinnatian. They were apparently part of the normal Cincinnatian fauna, and, as is the case
with more well-documented “normal” occurrences (e.g. Holland et al., 2001; Holland and
Patzkowsky, 2007), the taxonomic assemblage of occurrences of the “Cyclora fauna” is variable
as well. They also frequently contain faunal elements not represented among the larger fossils.
This suggests that taphonomic, rather than ecological processes, generated the phosphate-rich
beds in which these diminutive steinkerns are visibly concentrated.

Cincinnatian limestones probably resulted from prolonged periods of low sedimentation
where shells accumulated, and the accumulations were episodically disturbed by tropical storms
or tsunamis (e.g. Brett et al., 2008; Dattilo et al., 2008, 2012). We hypothesize that under these
circumstances, the relatively high durability of CFA as compared to calcite and especially
aragonite would lead to continued accumulation of newly formed phosphatic particles.
Meanwhile, the destruction of shelly particles would have previously reached equilibrium with
their production. In this paper we specifically illustrate steinkerns found in the context of original
shell material, but work in progress (Dattilo et al., 2015a, 2015b; Reeder et al., 2015) reveals that
many phosphatic grains are separated from their original calcareous skeletal materials,
suggesting a direct relationship between phosphate content, limestone maturity, and shell
destruction.

Small Mollusks are Everywhere

Even if a major portion of the Ordovician Cyclora fauna were derived from diminutive
adults, this would not constitute evidence of a Lilliput fauna. Micromollusks are a major but
understudied component of normal marine faunas both fossil (Garvie, 2008) and recent (Hickman,
2008). In a large-scale study of the molluskan fauna of New Caledonia, Bouchet et al. (2002) found
that the adult sizes of 2581 species of mollusks range from 0.4 to 450 mm, with half the species
under 8 mm, and 33.5% below 4.1 mm. Our own observations on San Salvador Island, Bahamas
confirm this: gastropods less than 4 mm in size are abundant in nearshore environments. This
conclusion accords with Redfern (2001) who studied mollusks on Abaco, another Bahamian island, from
1964 to 2001. We calculate a median shell size of 7 mm for the over 700 species of shelled gastropods he
reported (Redfern, 2001). Since this value refers to the maximum sizes observed on Abaco over a period
of almost four decades, the median size of the actual populations must be significantly lower. These case
studies imply that a fossil assemblage consisting of small mollusks could result from sampling
bias alone (compare Brayard et al., 2015). As Brayard et al. (2010) argued in the controversy over
the significance of the apparent size reduction of mollusks following the P-T mass extinction
(Nützel et al., 2010; Brayard et al., 2010; Fraiser et al., 2011; Brayard et al., 2011), a diminutive
fauna is characterized not by the presence of small species or specimens, but by the absence of
large ones. As demonstrated by partial preservation, normal sized faunal elements are generally
present in the Ordovician phosphatic fossil assemblages. We find no evidence to support the idea
that the original biological communities consisted of unusually small-bodied forms. However,
given the well-known bias against the preservation of small mollusks as calcareous fossils (e.g.
Valentine et al., 2006), some of which may result from collection bias (e.g. Cooper et al., 2006), 
easily-processed phosphatic steinkerns of common smaller forms may provide a window into a 
relatively poorly-understood aspect of ancient normal marine communities.

Modern Oxygen-stressed Faunas are not Characterized by Lilliput Mollusks

Witzke and Heathcote (1997) suggested that the diminutive phosphatic mollusk fossils of 
the coeval Maquoketa formation in Iowa might be explained by benthic community development 
in or near oxygen deficient water associated with upwelling. However, even if the Cyclora fauna 
were fully constituted of dwarfed forms, studies of modern communities do not support the 
conclusion that the original environment was oxygen stressed. The environmental impacts of 
human-induced oceanic hypoxia is a focus of current oceanographic research (Diaz, 2001; Gray 
et al., 2002), but natural oxygen minimum zones (OMZs) provide the most appropriate modern 
analogues of ancient, putatively oxygen-depleted marine environments. OMZs are relatively 
stable O2-deficient water strata that develop beneath productive surface waters, generally 
associated with upwelling (Levin, 2003), at depths mostly between 100 and 1500 m. They 
occupy large areas of the East Pacific, the Bay of Bengal, the Arabian Sea, and a smaller zone of 
the southwest African continental margin (Paulmier and Ruiz-Pino, 2009). Transects taken 
across OMZs show established benthic communities across relatively stable gradients from fully 
oxygenated surface waters to near total anoxia and back to oxic conditions at depth. A trend to 
smaller individual body masses towards the OMZ center has been documented in some cases 
(Quiroga et al., 2005; Murty et al., 2009; Gooday et al., 2009; Cowie and Levin, 2009) but was 
not found in others (Levin et al., 2000, 2002; Hughes et al., 2009). Such discrepancies suggest 
that even under permanent severe hypoxia, additional factors, for example food availability, may 
control community composition (Levin et al., 2000, 2009). It cannot be overstressed that in the
above cited cases where O₂-correlated size decreases were detected, the effect resulted from
shifts in community composition but not from dwarfing or paedomorphosis of individual species.
Among metazoans, soft-bodied taxa dominate central parts of OMZs while calcified forms
generally are rare or absent (reviewed by Levin, 2003; for an analogous conclusion concerning
continental shelf anoxia, see Tyson and Pearson, 1991). A remarkable exception is the shelled
gastropod, *Tibia delicatula*, which has been collected from the OMZs off Oman and Pakistan at
minimum O₂ levels of 0.16 and 0.11 ml O₂ L⁻¹, respectively (Ramirez-Llodra and Olabarria,
2005). Mature animals of over 60 mm shell length were present, but two thirds of the populations
fell into the immature size class of 10 to 23 mm shell length. Such dominances of immature size
classes are common and occur also in snails inhabiting the intertidal, arguably the best
oxygenated marine habitat (for an example, see Cyrus et al., 2015). More importantly, no signs
of dwarfism or pedomorphosis were detected, as only individuals of over 62 mm had fully
developed gonads (Ramirez-Llodra and Olabarria, 2005). Taken together, recent ecology does
not support the notion that O₂-deficient habitats are characterized by large densities of dwarfed
or pedomorphic, shelled mollusks.

**Phosphogenesis was not Unusual**

Ultimately the idea that phosphatic fossil assemblages represented oxygen-stressed
benthic communities (e.g. Snyder and Bretsky, 1971) was derived from the upwelling model of
phosphogenesis (Kazakov, 1937). Our field area was in a shallow (generally 30 m or less; Vogel
and Brett, 2009) epeiric sea far from the edge of the shelf. Upwelling in such an area seems
unlikely, but even if it did occur (Hermann et al., 2004), excess phosphorus would have triggered
phytoplankton blooms and the formation of phosphorites along the margin of the shelf, a process
that happens today in water depths >100 m (e.g. Montiero et al., 1983; Setty, 1983; Garrison,
1992; Glenn et al., 1994; Heggie et al., 1990). This study, along with mounting evidence against
Ordovician (Katian) Laurentian cooling (e.g. Quinton and MacLeod, 2014; Hughes et al., 2015)
argues against the upwelling model. In modern continental shelf environments phosphogenesis
may occur even in non-upwelling environments (Ruttenberg and Berner, 1993). The ubiquity of
the phosphatic small shelly fossils in the Cincinnatian, combined with a sedimentary model for
phosphate concentration, suggests that phosphogenesis was an ongoing process operating under
the normal epeiric sea conditions, and that the richly phosphatic beds are formed by long periods
of low sedimentation rather than incursions of unusual water masses. Therefore, it is not
necessary to invoke low-oxygen water masses or upwelling to explain the occurrence of these
strata.

Implications for Cambrian Small Shelly Faunas

The small shelly fauna of the Cincinnatian are similar in size to the better known small
shelly faunas of the Cambrian, particularly those of the Tommotian, which mark the beginning of
the Cambrian explosion (e.g. Bengtson et al., 1990). However, it has been suggested that this
style of preservation had all but disappeared by the Middle Cambrian (Porter, 2004). Recent
work on the taphonomy of the Cambrian small shelly faunas (Creveling et al., 2014) has revealed
patterns of preservation that are virtually identical to these Ordovician small shelly fossils. In
both cases, CFA selectively precipitated in skeletal spaces of certain small sizes, and in both
cases, silt infillings often further reduced the size of the pores within the cavity. The similarity in
preservation raises the possibility that the “phosphatization taphonomic window” (Brasier, 1990)
had not necessarily closed by end-Cambrian.

The Cincinnatian small shelly fossils, because of the unique size selectivity of the
taphonomic process, preserve small individuals and forms that would not otherwise have been
preserved among the larger forms in the same communities. This raises the question as to whether the phosphatic small shelly faunas of the early Cambrian are representative of the original shelly faunas, or if taphonomic bias in phosphatic molding preferentially preserved only the smaller elements of a more diverse original fauna as well (Mus et al., 2008).

CONCLUSIONS

Preliminary studies suggest that small, sand-sized steinkerns of gastropods, bivalves and other fauna are present in most Ordovician shell-bed limestones of the Cincinnati area, even though they are only visibly concentrated in a few of these beds. We were able to study the morphology of these phosphatic fossils through analysis of thin sections and insoluble residue from these limestones. In no case were we able to demonstrate that the fossils were truly dwarfed, and in many cases we are able to demonstrate that the phosphatic steinkerns had formed in small parts of larger shells. The presence of these partially-molded larger forms speaks against a diminutive fauna.

Our observations indicate that the size distribution of individuals in phosphatic steinkern assemblages do not reflect the size distribution of individuals in the original fauna but resulted from taphonomic bias. The phosphogenic process appears to be restricted to filling sand-sized or smaller pores in the Cincinnatian. Once precipitated, phosphate minerals were more resistant to sedimentary reworking than aragonite or calcite. This allowed the steinkerns to be concentrated while calcareous shells were destroyed by repeated reworking of the sea-floor during times of low siliciclastic input.

Given the prevalence of small (<4 mm) adult mollusks in modern normal marine environments, a large number of small species must be expected in ancient normal marine
environments, and phosphatic preservation provides a taphonomic window into this frequently overlooked ecological component. Furthermore, the ecology of modern oxygen minimum zones suggests that shell-bearing metazoans generally are rare in oxygen-depleted environments. Thus, even if the Ordovician faunas could be demonstrated to be truly dwarfed, by comparison with modern faunas, the relative abundance of shelled mollusks would still suggest normal oxygen levels in the benthic environment (although not necessarily in the sediment), and argue against water-column hypoxia. If this is true, major paleoclimatic or oceanographic interpretations based on the presence or absence of the “Cyclora fauna” are unwarranted.

Finally, the taphonomic processes that led to the formation of the Cyclora fauna are similar if not identical to those that led to the more familiar Cambrian small shelly fauna, as well as numerous other reported occurrences of small phosphatic steinkerns. This suggests that the Cambrian does not represent a “taphonomic window” with respect to small “shellies,” but that small shellies are a common but overlooked Phanerozoic phenomenon.

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FIGURE 1—Map showing paleogeographic setting and localities, with abbreviations, for figured specimens: Lawrenceburg, Indiana (LBG 36.5); Christ Hospital, Cincinnati, Ohio (CHS); Harsha Lake, Ohio, (HRL): Fredericktown, Kentucky, (FRD 16.6); Florence Freedom Ball Park, Kentucky (FFP); US 421 road cut just south of Milton, Kentucky, (MLT); US 421 roadcut at Madison, Indiana (MAD 5.5). Metropolitan areas of Cincinnati, Louisville, and Lexington are shaded in the locality map.

FIGURE 2—Stratigraphic column showing the traditional stratigraphic subdivisions of the Cincinnati Ordovician and the approximate stratigraphic distribution of the samples examined in this study. Miamitown = Miamitown Shale Member of the Fairview Formation; MHB = Marble Hill Bed of the Liberty Formation. See Figure 1 for locality abbreviations.

FIGURE 3—Two halves of *Lunatia heros* (Northern Moon Snail) with artificial silicone steinkerns showing mold of apertural lip (alm) and umbilical cavity (uc). A) Rubber shell cavity mold (scm) resting in one half of the shell, with a visible imprint of the apertural lip (alm). B) Apertural lip (al) itself on the other side of the shell, shell cavity (sc), and umbilical cavity (uc). C) Umbilical mold (um) in position inside of transparent shell-cavity mold. All figures to scale.

FIGURE 4—Direct evidence of incomplete gastropod steinkerns (“teilsteinkerns”). All specimens are from MLT (Fig. 1). A–B) Thin section views of gastropods incompletely filled with phosphate; A) meniscate fill with deep center (mc) and edge (me); B) non-meniscate edge (e). C–D) Phosphatic gastropod teilsteinkern terminating in smooth, sharp-edged meniscus-like surface. E–F) Two specimens with partial, unbroken steinkerns terminated at both ends by
meniscate surface. G–H) Details of either end of F. A–C, E to scale with black 1mm scale bar; F; D, G, and H enlarged, each with white 500 µm scale bars.

**FIGURE 5**—Comparable whorls of a larger and smaller *Lunatia heros* illustrating how apex is occluded by secondary shell accretion throughout ontogeny. 1 cm scale bar applies to whole shell insets; 1 mm scale bar applies to enlarged views.

**FIGURE 6**—Macroscopic gastropods from the Marble Hill Bed at Bedford, Kentucky (A–D; Roadcut on US Highway 42, 4 km east of US Highway 421, 38.625000°N, 85.250000°W), and from the Waynesville Formation near Rectorville, Kentucky (road cut on Kentucky Highway 9 just east of Bridgeport Road 38.567617°N, 83.642235°W). Thin section (A,C,E) with respective tracings (B,D,F) showing the distribution of primary and secondary shell. A–B) *Paupospira bowdeni* (Safford, 1869. C–D) *Clathrospira conica* (Ulrich & Scofield, 1897), E–F) *Cyclonema* sp., All figures to scale.

**FIGURE 7**—Gastropod steinkerns with differing apical geometries arranged in order of what is inferred to be progressive apical occlusion. All specimens are from sample FRD 16.6 (Fig. 1), and illustrated to scale.

**FIGURE 8**—Cartoon showing how progressive ontogenetic occlusion (A–E) of the apex of the shell cavity affects the shape of the steinkern. Top row represents teilsteinkerns; bottom row represents corresponding original shells.

**FIGURE 9**—Umbilical steinkerns of gastropods. A–C) Thin-section views of associated phosphatic shell-cavity and umbilical-cavity steinkerns from Madison, Indiana (MAD 5.5, Fig. 1). A and B are axial sections; C is a transverse section. Remaining specimens are from Milton,
Kentucky (MILT, Fig. 1). D–E) Small umbilical steinkerns from acid residue. F–G) Largest umbilical steinkerns from acid residue. H) Oblique thin-section of shell-cavity and umbilical steinkern. I) Thin section of much larger phosphatic umbilical steinkern with outer walls and shell cavity of the gastropod taphonomically destroyed before final burial. J) Adapical view of associated shell-cavity and umbilical steinkerns showing large flange and imprint of external growth lines. K–L) Apical view showing geometric relationship between umbilical and shell-cavity steinkern (K) and imprint of external ornament (L). M–N) Flange of umbilical steinkern showing up between whorls, with detailed impression of delicate external ornament. All figures to scale of black 1 mm scale bar except enlarged views L and M, each with an individual white 200 µm scale bar.

**FIGURE 10**—Monplacophorans from Cincinnati, Ohio (A; CHS, Fig. 1.) and Milton, KY (B–E; MLT, Fig. 1) A) Near-axial section through mostly carbonate sediment-filled (cf) shell showing a dark 1.2 mm phosphatic teilsteinkern in a 12 mm shell as reconstructed from partially preserved final whorl (fw). B) Axial section through a phosphatic steinkern showing lack of secondary thickening, unfilled, partially preserved final whorl (fw), and umbilical steinkern (us), C) Large steinkern showing wavy meniscate termination and umbilical steinkerns (us) that record the former presence of at least a half whorl of additional shell. D) Smaller steinkern whose umbilical steinkern (us) component records the former presence of a full extra whorl. E) Smaller steinkern showing bulbous protoconch at the apex. A enlarged half scale, with white 1 mm scale bar. All others to scale of black 500 µm scale bar.

**FIGURE 11**—Bivalve fossils. A–E) Assorted steinkerns of smaller bivalves from Milton, KY (MILT, Fig. 1). F–G) Two views of a phosphatic mold, probably from the hinge teeth of *Lyrodesma* from Florence Freedom Park (FFP, Fig. 1). H–I) Hinge area of a calcitic
(recrystallized from aragonite) *Lyrodesma* from the Kope Formation, Carrollton, Kentucky showing spaces that correspond to molds F–G. J–L) Associated clusters of hinge-teeth molds from Florence Freedom Park (FFP), with gastropod embedded within the meniscate open edge of L. All figures to scale.

**FIGURE 12**—A–F) Echinoderm ossicles from Milton, Kentucky (MILT, Fig. 1). A–B) Thin section showing stereom mold. C) Columnal of *Cincinnaticrinus*. D) Partial columnal from larger camerate crinoid. E) Columnal of *Xenocrinus*. F) Arm facet of unidentified crinoid. G–L) Bryozoan zooecia from Milton, Kentucky (MILT, Fig. 1). G–H) Thin section views of two different species of bryozoans showing differing degrees of phosphatic infilling. I–K) Intact bryozoan colony steinkerns from acid residue representing a variety of species. L) Detail of meniscate termination of phosphatic fill on bryozoan steinkerns from acid residue. Black 500 µm scale bar applies to all figures except enlargements B and L, which have individual scale bars.

**FIGURE 13**—Normal-sized fauna recorded as molds of intragranular and intergranular porosity from Milton, Kentucky (MILT, Fig. 1) A) Thin section showing fragment of the brachiopod *Rafinesquina* with phosphatic mold of “Trypanites” boring (b) and a thin phosphatic mold of the internal surface (i) formed where another fragment lies close. B) Thin section showing space between two brachiopod fragments filled with phosphate. C) Intergranular mold of *Rafinesquina* ornament from acid residue. D) Trilobite fragment preserved as intragranular mold, E) Thin section through trilobite showing phosphatic filling within “crook” area (cutical pores are darkened by linings of disseminated pyrite framboiids). All figures to scale.
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