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THE "CURSE OF *RAFINESQUINA*:" NEGATIVE TAPHONOMIC FEEDBACK EXERTED BY STROPHOMENID SHELLS ON STORM-BURIED LINGULIDS IN THE CINCINNATIAN SERIES (KATIAN, ORDOVICIAN) OF OHIO

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ABSTRACT

Thousands of lingulid brachiopods were found clustered beneath hundreds of individual valves of the strophomenid brachiopod *Rafinesquina* in the Upper Ordovician of Ohio. This association suggested a relationship between the two brachiopods, but the nature of this relationship was unclear. We utilized serial thin sectioning to examine these brachiopods and to determine the origin of the bed in which they were found. Sedimentary structures, mixed taphonomies, and stratigraphic and paleogeographic setting suggest that the lingulids occupied a hiatal concentration that had previously been reworked, but not significantly transported, by tropical storms. The final burial event was a storm that exhumed living lingulids along with disarticulated *Rafinesquina* shells from the same sediments. Neither living nor dead shells were transported, but were reworked locally, then reburied together. The lingulids then burrowed upward to escape, but most were trapped by the concave-downward *Rafinesquina* shells that had been redeposited above them. This finding offers the first documented example of negative ecosystem engineering and taphonomic feedback in the fossil record, as well as the oldest documented lingulid escape traces. It also suggests that taphonomic feedback can be subdivided into live-dead interactions that occur under normal background depositional conditions and those that occur during periodic short-lived sediment-reworking events, such as storms and tsunamis.

INTRODUCTION

Taphonomic feedback (Kidwell and Jablonski, 1983; Kidwell, 1986a, 1986b) is the idea that accumulation of organic remains either enhances the habitat for some organisms (positive taphonomic feedback), and/or degrades the habitat for others (negative taphonomic feedback). Examples of epibionts living on skeletal remains are direct evidence of positive taphonomic feedback (e.g., Kidwell and Jablonski, 1983; Kidwell, 1986b; Meyer, 1990; Shroat-Lewis et al., 2011). Disruption of infaunal burrowing activities by skeletal fragments is an example of negative taphonomic feedback (Peterson and André, 1980; Reise, 2002); direct fossil evidence of this phenomenon has not been documented previously. Infaunal organisms are vulnerable to exhumation (Shäfer, 1962; Boyajian and Thayer, 1995; Cleveland et al., 2002; Zonneveld and Greene, 2010; Harper et al., 2012) or entombment (Schäfer, 1962; Schulenberger, 1970; Kranz, 1974; Nichols et al., 1978; Peterson, 1985; Maurer et al., 1986) during storms or other sediment-disturbing events, but organisms that burrow can also re-establish viable life positions subsequently (Shäfer, 1962; Maurer, 1967; Schulenberger, 1970; Kranz, 1974; Nichols et al., 1978; Maurer et al., 1986).

We describe an unusual association of intact lingulid brachiopods (cf. *Pseudolingula* sp.) clustered beneath the disarticulated shells of the strophomenid brachiopod *Rafinesquina* in a storm-reorganized shell bed from the Upper Ordovician near Cincinnati, Ohio (Fig. 1). *Rafinesquina* was named for Constantine Rafinesque, a 19th-century naturalist who, upon expulsion from his position as professor at Transylvania University in Lexington, Kentucky, pronounced a curse on the institution (Rafinesque, 1836; Boewe, 1987). Folklore has attributed to this curse a string of tragic deaths and other misfortunes continuing to the present day. We present evidence that his namesake brachiopods, with strange parallels to the historical figure, exercised the ecological analogue of a curse (see Appendix, p. 372) on their environment, long after they themselves had died.

It appears that the small burrowing cf. *Pseudolingula* sp. existed among large *Rafinesquina* shells until a storm buried many of them. The lingulids then burrowed upward to escape, only to be trapped beneath a freshly redeposited *Rafinesquina* shell pavement. Their death traces extend the record of upward escape-burrowing capabilities of lingulid brachiopods into the early Paleozoic and are direct evidence of a negative taphonomic feedback mechanism by which infaunal escape behaviors were rendered ineffective by the presence of skeletal debris.

BACKGROUND

Burrowing Abilities of Early Lingulids

Benthic organisms living in shallow marine settings are vulnerable to entombment or obrution (Brett and Seilacher, 1991) by sediments deposited by storms (Brett et al., 2008; Dattilo et al., 2008, 2012), tsunamis (Pratt and Bordonaro, 2007), and in the modern world, dredge spoil disposal (e.g., Maurer et al., 1986). The response of modern sessile epifauna such as bivalves (Kranz, 1974) or corals (Bongaerts et al., 2012) to such an event is, at best, limited. Escape structures associated with epifaunal organisms are rarely documented in the fossil record, although a weak escape ability has been documented for some strophomenate brachiopods (Dattilo, 2004; Dattilo et al., 2009).

Infaunal organisms such as lingulid brachiopods and bivalves are especially vulnerable to such events, because either entombment or exhumation can prove fatal (Shäfer, 1962; Maurer, 1967; Schulenberger, 1970; Kranz, 1974; Thayer and Steele-Petrović, 1975; Nichols et al., 1978; Peterson, 1985; Maurer et al., 1986; Boyajian and Thayer, 1995; Cleveland et al., 2002; Zonneveld and Greene, 2010). However, burrowing infaunal organisms are also more likely to be physically capable of responding to entombment or exhumation than epifaunal organisms. For example, when modern lingulids re-burrow after exhumation, they first dig downward and then turn upward, forming a U-shaped burrow (Paine, 1963; Thayer and Steele-Petrović, 1975; Savazzi, 1991). If entombed, they burrow upward (Yatsu, 1902; Paine,

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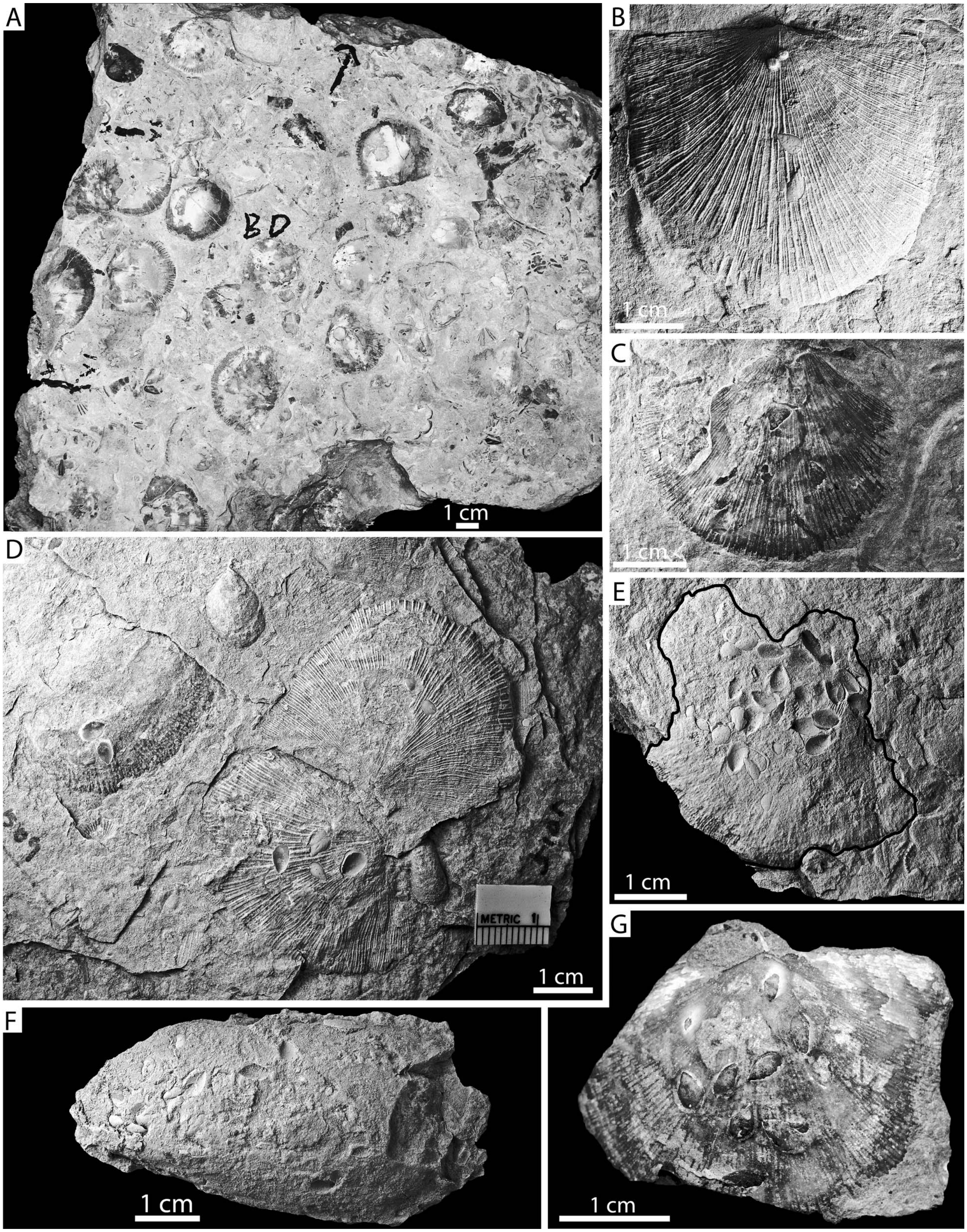

FIGURE 1—Samples initially collected from the study area. All samples are from the same bed. A) View of bedding plane with abundant *Rafinesquina*, USNM #553366. B) *Rafinesquina* with encrusting *Sphenothallus* and lingulids beneath, USNM #553367. C) *Rafinesquina* with hints of burrows beneath, USNM #553368. D) Three *Rafinesquina* with many lingulids clustered beneath, USNM #553369. E) Partially exposed and spalled *Rafinesquina* with abundant lingulids beneath, line denotes extent of exposed *Rafinesquina*, USNM #553370. F) Bivalve (*Modiolopsis*?) with lingulids beneath, USNM #553371. G) *Rafinesquina* with abundant lingulids beneath, USNM#553372.

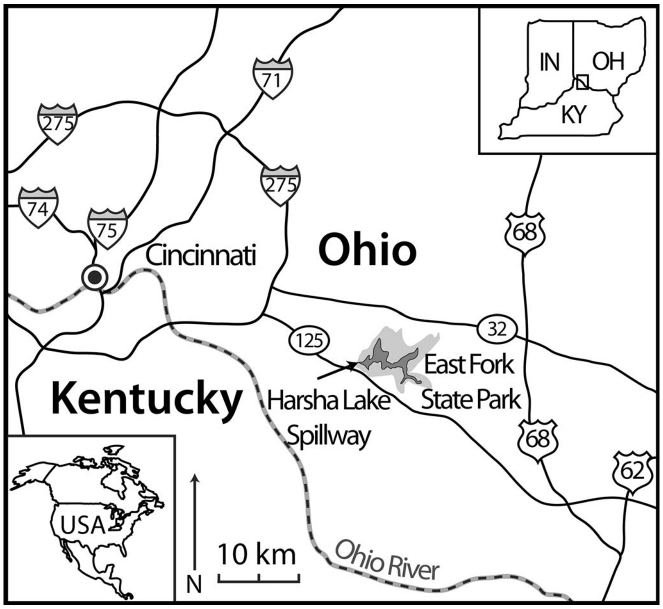

FIGURE 2—Location of study area. The specimens were collected in the spillway of Harsha Lake to the southeast of Cincinnati, Ohio. Lower left box indicates position of upper box, which indicates position of study area.

1963; Thayer and Steele-Petrović, 1975; Emig, 1983; Hammond, 1983). Triassic trace fossils provide the oldest record of this ability recorded to date (Zonneveld and Pemberton, 2003; Zonneveld et al., 2007; Zonneveld and Greene, 2010); however, evidence suggests that at least some lingulids functioned as infaunal filter feeders as early as the early Cambrian (Pemberton and Kobluk, 1978).

Taphonomic Feedback and Ecosystem Engineering

The accumulation of shells has been suggested as a driving force behind successional-scale community change (e.g., Walker and Alberstadt, 1975; Harris and Martin, 1979). This taphonomic feedback (Kidwell and Jablonski, 1983; Kidwell, 1986a, 1986b) can both facilitate and inhibit the activities of subsequent community inhabitants. For example, accumulated shells may encourage the recruitment of epibionts while simultaneously inhibiting the activities of infaunal organisms. Facilitation has been documented frequently in the fossil record (e.g., Kidwell and Jablonski, 1983; Kidwell, 1986b; Meyer, 1990; Shroat-Lewis et al., 2011) and in the modern marine environment (e.g., Reise, 2002: Gutiérrez et al., 2003). The latter process has been documented infrequently in the modern environment (Peterson and André, 1980; Reise, 2002) and has not reported previously from the fossil record.

Taphonomic feedback is a subset of ecosystem engineering in which the activity of an organism controls access to a resource by other organisms within the ecosystem (Jones et al., 1994). In this case taphonomic feedback is autogenic ecosystem engineering (Jones et al., 1994) in that it is the growth of the shell or skeleton and its subsequent death that controls access to suitable substrate for living organisms within the community.

MATERIALS AND METHODS

Fossil Occurrence

Thousands of cf. *Pseudolingula* sp. with hundreds of *Rafinesquina* sp. (and a small number of other larger calcareous shells) were found on an approximately 4-square-meter exposed surface of a 3–6-cm-thick shell bed limestone, which was covered with a pavement of *Rafinesquina* (Figs. 1A, D). This bed occurs in the upper part of the Fairview Formation exposed in the spillway of Harsha Lake, Clermont County, Ohio (Fig. 2). The exposed surface was collected in several large slabs along with numerous individual isolated *Rafinesquina* specimens that had weathered free. The materials illustrated are reposited at the United States National Museum (USNM #553366–553373) and at the Cincinnati Museum Center (CMC #69083–69091).

Laboratory Methods

The Harsha Lake fossil bed was analyzed by slabbing to establish bedding scale relationships, serial sectioning to document the distribution of individual shells and burrows, and by dissolution in dilute acid to isolate lingulid valves for taxonomic identification.

Several vertical slabs (30 cm wide; Fig 3A) were cut from a larger (30 × 70 cm, 6-cm-thick) bed fragment. One slice was polished, etched, and peeled (Fig. 3A), and four additional slices were further sectioned to form the vertical bed serial set discussed below. Three horizontal slabs (Figs. 3B–D) were cut from another (21 × 19 cm) bed fragment, two thicker slices at the bottom and top of the bed, and a thinner slice bracketing approximately the horizon containing the most *Rafinesquina*. The upper surfaces of all three horizontal slices were polished.

Some fragments were sectioned serially, creating serial sets of thin sections and peels. To make these, samples were trimmed to fit small (2.5 × 4.5 cm), or large (7.5 × 5.5 cm) petrographic slides. The trimmed fragments were embedded in epoxy resin, the resin blocks were trimmed to size, and the trimmed blocks were sliced into wafers at 1.0–2.0 mm spacing using a Buehler IsoMet 1000 precision saw. These wafers were hand polished and affixed to slides that were then prepared as thin sections. We illustrate three serial sets (Figs. 4–6; Supplementary Data 1–3[1]).

1. One vertical serial set (set 1; Fig. 4; Supplementary Data 1[1]) was made from an isolated *Rafinesquina* valve that had weathered from the slab and was associated with several visible lingulids (Figs. 4A, H). 26 wafers were cut at 1.0 mm spacing, and mounted on small thin sections. This, along with 12 similar serial sets not illustrated, provides a three-dimensional visualization of the arrangement of lingulids immediately below the *Rafinesquina* valves.
2. One horizontal serial set (set 2; Fig. 5; Supplementary Data 2[1]) was made from a small bedding fragment that was trimmed vertically around a single *Rafinesquina* valve with a cluster of lingulids beneath. The underlying 3 cm bed was sectioned into 15 wafers at 2 mm increments. After each wafer was affixed to a large thin section, and before being ground to the appropriate thickness, the other side was polished, etched, and peeled. This resulted in 30 sections spaced, on average, 1 mm apart. This set provides a three-dimensional view of the bed below a single *Rafinesquina* shell.
3. One vertical bed serial set (set 3; Fig. 6; Supplementary Data 3[1]) was made from a rectangular area of four of the vertical bed slices mentioned above (each slice 5.5 cm wide and 4 cm thick). A length of 8.3 cm was cut into 37 wafers at 2.0 mm spacing (9 mm previously removed in slab saw cuts), and mounted on large thin sections. This set provides a three-dimensional view of the bed below the *Rafinesquina* pavement.

Some of the rock remaining from sectioning and trimming operations was dissolved in 10% acetic acid, yielding abundant fragments of the lingulid for identification (Fig. 7). All sections, thin sections, and peels were scanned, generating high-resolution images. Specimens were also photographed prior to sectioning, and some specimens examined using a Hitachi 4800 scanning electron microscope.

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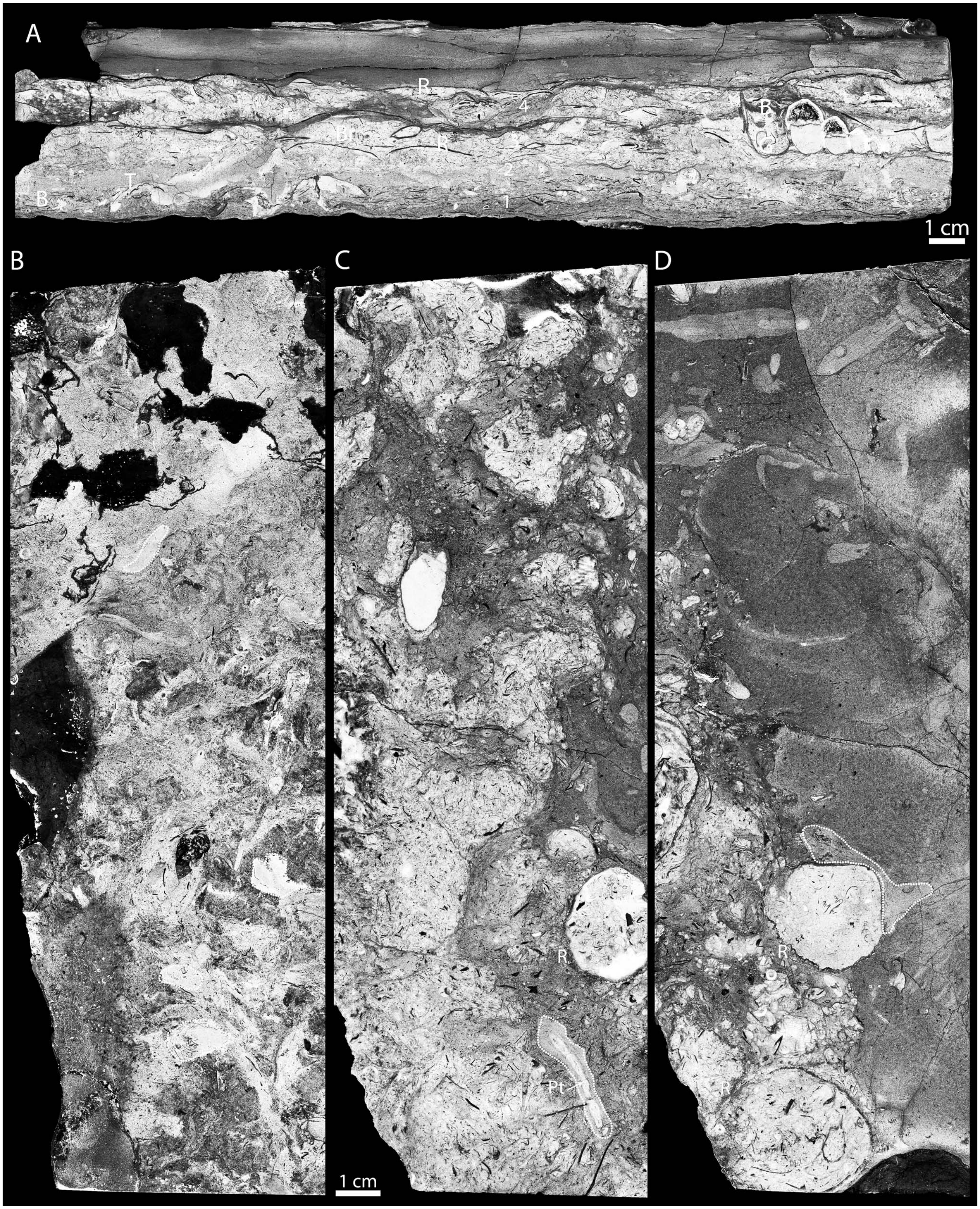

FIGURE 3—Polished slabs of the bed from which specimens were collected. Representative fossils only are labeled. B = brachiopods other than *Rafinesquina*, Br = bryozoan, G = gastropod, Pt = pedicle trace, R = *Rafinesquina*, and T = trilobite fragment. Selected burrow margins are outlined with a dashed line. A) Slab of bed cut perpendicular to bedding. The numbers 1–4 = four distinct units within the packstone portion of the bed. CMC #69083. B–D) Successive slabs cut parallel to bedding just below the highest occurrence of *Rafinesquina* in the uppermost part of the packstone unit (B), and through the boundary between the packstone and overlying muddy siltstone (C–D), CMC #69084.

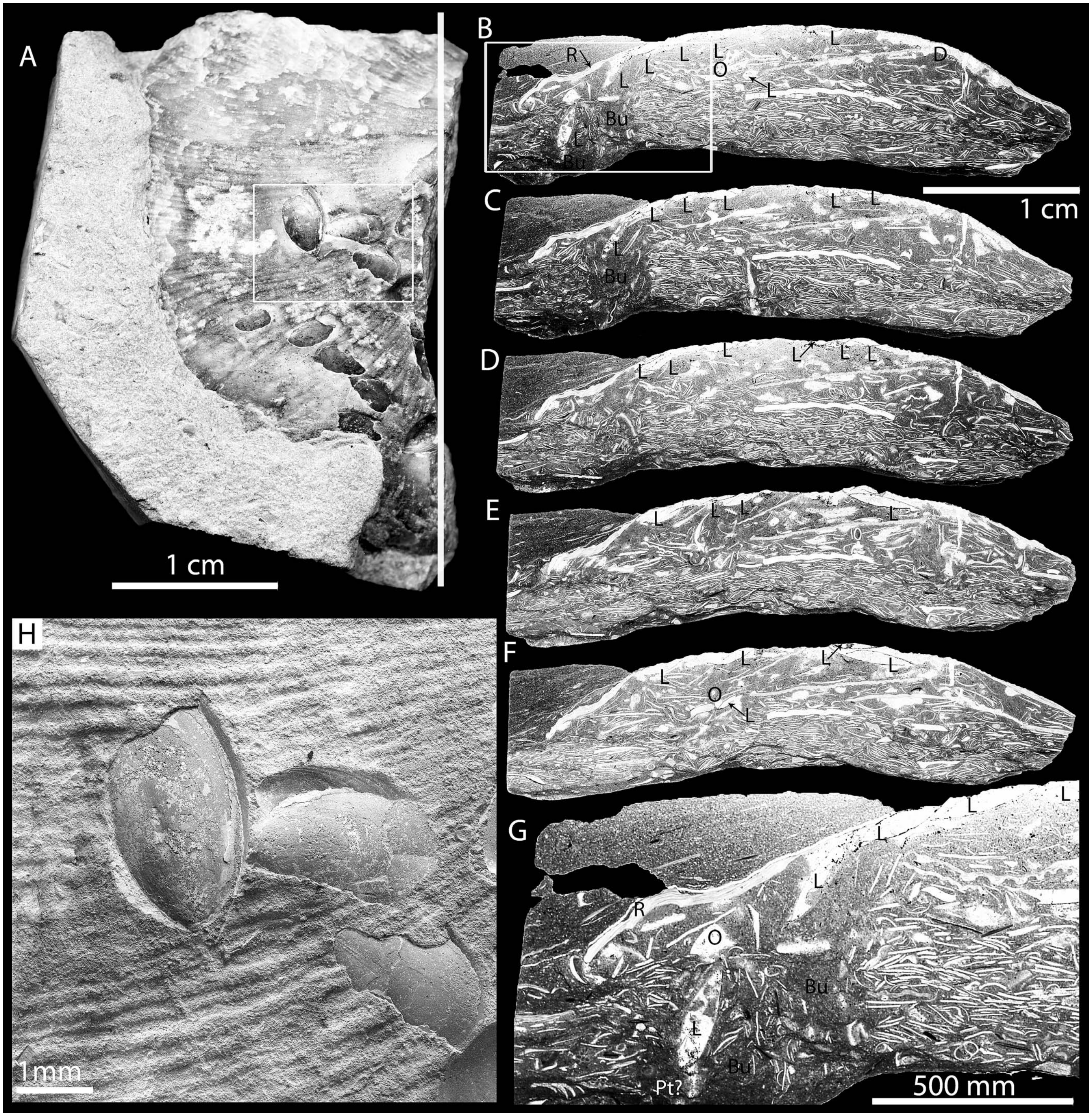

FIGURE 4—Specimen (USNM #553373) and selected vertical thin sections through it. The entire vertical valve serial set is available as Supplementary Data 1[1]. A) Specimen before sectioning. Area shown in box is shown in H. Vertical line shows orientation of sections. B–F) Thin sections spaced 1 mm apart. Scale bar for all to the bottom right of B. On all thin sections, lingulids = L and O = obstacles other than *Rafinesquina* with lingulids beneath. *Rafinesquina* shells = R and D = diagenetic cement. Box on figure B indicates view shown in view G. G) Detail of thin section B. H) Scanning electron microscope image of detail of A.

OBSERVATIONS

Occurrence of the Specimens within the Bed

The *Rafinesquina* are preserved as intact valves, partially spalled valves, and internal molds. A few specimens are encrusted with holdfasts of *Sphenothallus* (Fig. 1B) or small patches of bryozoans. Lingulid brachiopods are concentrated beneath the centers of the *Rafinesquina* shells (Figs. 1D–E, G). Lingulids also occur clustered beneath other concave-downward shells such as disarticulated shells of larger lingulid brachiopods, broken gastropod shells, and the bivalve *Modiolopsis* (Fig. 1F). The lingulids are extremely abundant where found, and can be associated with faint burrows visible on the surface of *Rafinesquina* internal molds (Fig. 1C). One partially exposed and spalled specimen of *Rafinesquina* (Fig. 1E) has at least 28 individual lingulids immediately beneath it. The majority of the lingulids are clustered beneath the concave side of either pedicle or brachial valves of *Rafinesquina*, none of which are obviously articulated. In contrast, lingulids are complete with either both shells in place or slightly askew, coated on the inside with fine pyrite, and filled with sparry cement. Although the lingulids are concentrated near the centers of the

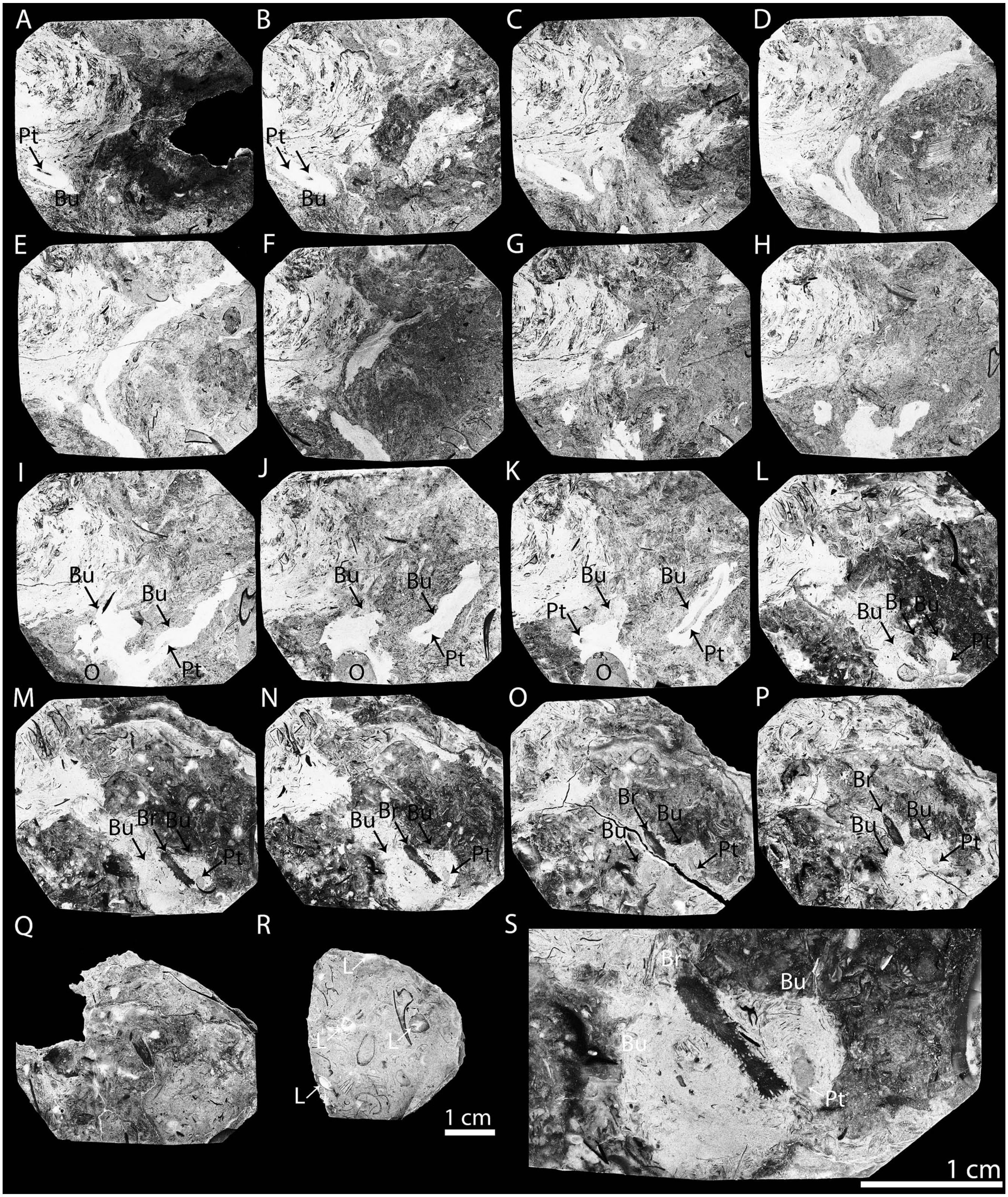

FIGURE 5—A–R) Selected sections from the horizontal serial set showing scans of surfaces before being ground into thin sections. The resulting thin sections and associated acetate peels are reposited as CMC# 69085, and the entire serial set is available as Supplementary Data 2[1]. A–K are from 30–20 mm below the uppermost *Rafinesquina*, spaced 1 mm apart. L–Q are from 10–5 mm beneath the uppermost *Rafinesquina*, spaced 1 mm apart. R is from 3 mm beneath the top of the *Rafinesquina*. S) Detail of N showing two lingulid burrows deflecting to the left and right of a ramose bryozoan. On selected sections, burrows = Bu, a pedicle trace = Pt, O = obstacle, Br = bryozoan, and L = lingulid.

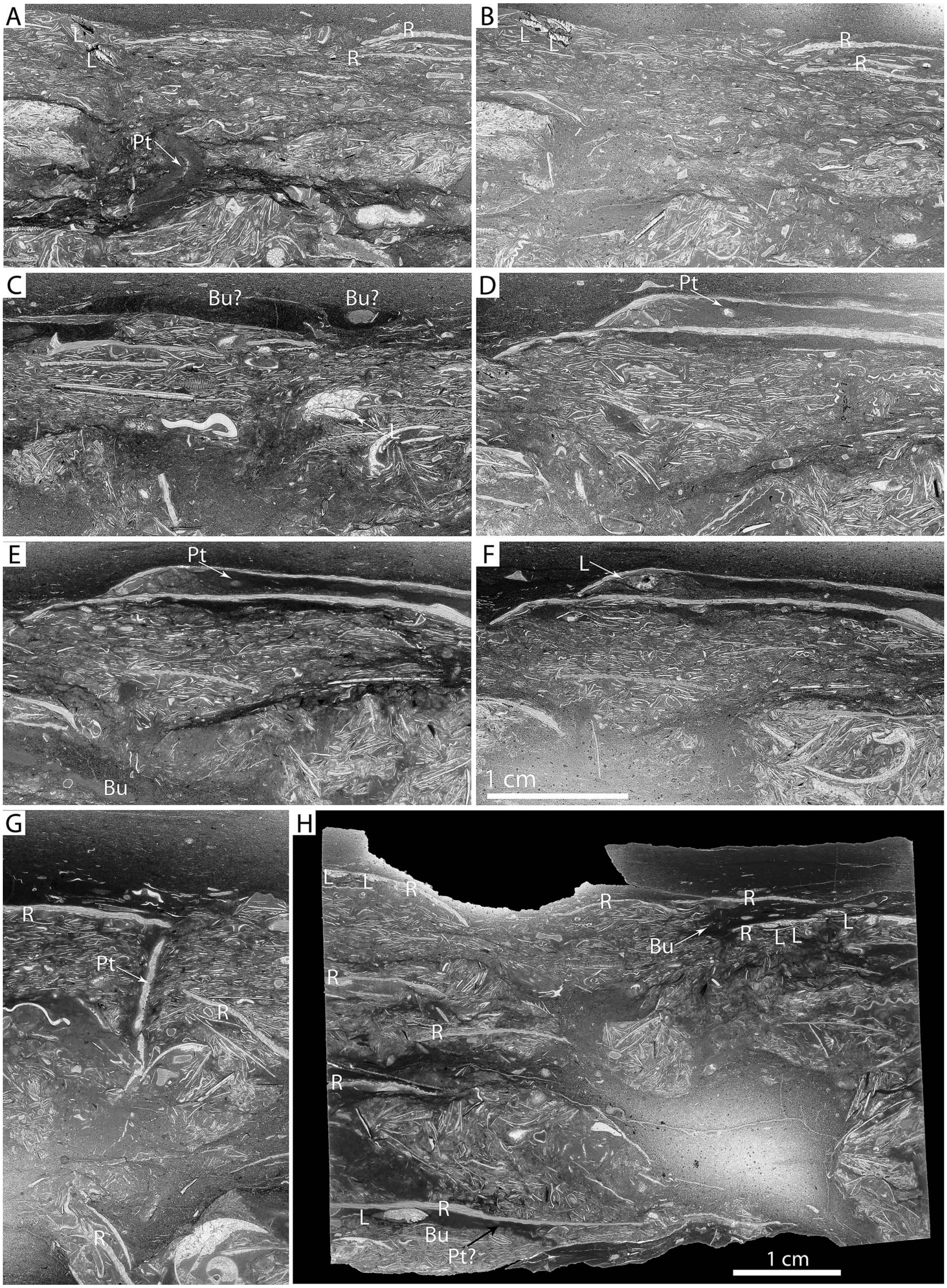

FIGURE 6—Selected vertical thin sections from the vertical bed serial set illustrating the shell bed, CMC# 69086. The entire series is available as Supplementary Data 3[1]. A–B) Two successive sections separated by 2 mm. C) Detail of thin section. D–F) Details of three successive thin sections separated by 2 mm. G) Detail of thin section. Scale bar for A–G is located at the bottom left of F. H) Entirety of a thin section. L = lingulids, R = *Rafinesquina*, Bu = burrow, and Pt = pedicle trace within a burrow. Bright area in lower right is caused by a thinning of the thin section.

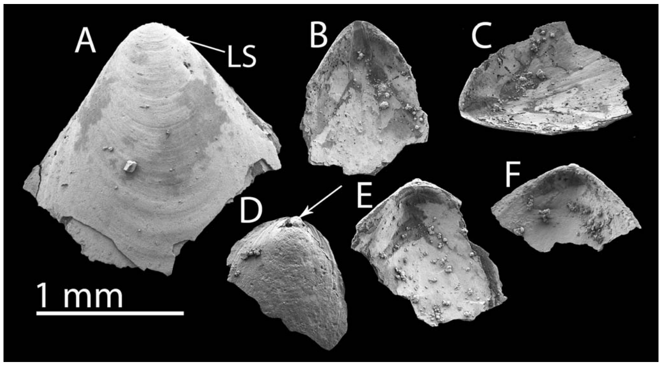

FIGURE 7—Fragments of *Pseudolingula* sp. from insoluble residue. A) Ventral valve exterior, CMC #69087. LS = interpreted edge of larval shell. B–C) Ventral valve interior, oblique view of pedicle valve interior, CMC #69088. D) Dorsal valve exterior, CMC #69089. Arrow indicates location of distinctive knob at dorsal beak. E) Dorsal valve interior, CMC # 69090. F) Dorsal valve interior, CMC# 69091.

Rafinesquina shells, they have no preferred orientation relative to the line of the commissure. When individual valves can be identified, no preferred orientation of the lingulid valves is apparent; approximately equal numbers of pedicle and brachial valves are juxtaposed against the *Rafinesquina* valve surfaces. All intact lingulids observed were beneath a valve of *Rafinesquina* or another taxon.

Description of the Bed

The resistant bed (Fig. 3A) consists of a shelly packstone component (3–4 cm thick) draped by a laminated muddy siltstone component (~2 cm thick). This bed is sandwiched between two clay-rich mudstones, each several centimeters thick. The basal contact with the underlying mudstone is sharp. The overlying mudstone was removed from the specimens by erosion prior to collection, but the siltstone fines upward into more clay-rich material, suggesting a gradational contact. A pavement of *Rafinesquina* shells with lingulids marks the upper surface of the shelly phase, and the bed tends to split on this boundary with the packstone below, and the laminated siltstone above. There is no evidence for erosion or discontinuity at this contact, as the matrix of the upper part of the packstone and the filling of the burrows matches the lithology of the siltstone. The tendency to split may be caused by differential expansion of clay, and almost certainly contributed to the spalling of *Rafinesquina* shells, with the upper part of the shell adhering to the siltstone, and the lower part to the packstone.

Within the resistant packstone, the polished vertical slab (Fig. 3A) shows shells and fragments arranged in four horizontal bands (labeled 1–4 on Fig. 3A), two containing packstone with micritic matrix and two containing packstone with more terrigenous matrix, similar in composition to the laminated siltstone. The basal unit is a micritic packstone consisting mostly of smaller fragments, the second unit is a dominantly siliciclastic unit with relatively few fossils. The third unit is micritic and contains the larger platy fossils such as *Rafinesquina* and other large fossils. The fourth unit is terrigenous, contains many fragmented molluscs, and is both underlain and overlain by *Rafinesquina* pavements. Burrows are present throughout all units of the packstone. The laminated muddy siltstone above the packstone contains burrows but few other fossils.

Polished horizontal slabs cut through the boundary between the *Rafinesquina* shell–dominated packstone and the overlying muddy siltstone revealed more about the relationship between the two (Fig. 3B–D). The lowest slab (Fig. 3B) cuts through the uppermost part of the packstone and reveals traces of irregular burrows. The two slabs above (Fig. 3C–D) reveal the gradational and irregular contact between the two units. The muddy siltstone layer is heavily burrowed and some burrows can be traced from the packstone into the muddy siltstone above (Fig. 3B–D). The burrows are both horizontally and vertically oriented.

Shelter porosity is seen beneath shells, especially in the upper part of the packstone portion of the bed (Figs. 3A, 4B–G). This structure is usually interpreted as evidence of concentration of shells as the result of a tropical storm as documented in other Cincinnatian beds (see Dattilo et al., 2008, 2012, and references therein). The gradational contact between the fossil-rich packstone below and the fossil-poor muddy siltstone above (Figs. 3A–D), the infiltration of sediment from the siltstone to the packstone, the siltstone filling of the burrows within the packstone, as well as the apparent continuation of escape burrows from one unit to the next suggest a common origin for these two successive units. Shell bed–laminated couplets, interpreted as single storm deposits, are well documented (e.g., Kreisa, 1981; Kreisa and Bambach, 1982).

Although the uppermost part of the packstone consists of many whole *Rafinesquina* valves, the majority of the shell material within the packstone actually consists of less-identifiable fragments. Differential preservation of the shell material indicates a long period of exposure to reworking prior to the final depositional event. Small shell fragments, and fragmental, disarticulated *Rafinesquina* are preserved together with perfectly preserved lingulids. The exquisite preservation of the small, fragile lingulids rules out the storm as the cause of the fragmentation and disarticulation of the *Rafinesquina* shells, and suggests that the *Rafinesquina* shells were affected by previous disturbance events. The abundance of shell fragments relative to whole shells in the bed suggests that the strata were shell-rich before the storm occurred and therefore likely experiencing a reduced rate of clastic sedimentation. In summary, the packstone and overlying siltstone represent a hiatal concentration remodeled into an event concentration (Kidwell, 1991; Dattilo et al., 2012).

Differential Preservation of the Strophomenid and the Lingulid

In thin section, all lingulids encountered in this study are articulated and filled with sparry cement, whereas all *Rafinesquina* are disarticulated (Figs. 4–6, Supplementary Data 1–3[1]). In many cases a thin veneer of diagenetic cement coats the downward side of the *Rafinesquina* valves and may incorporate articulated lingulid valves within, leaving the appearance of the latter having been incorporated into the shell of the former (Figs. 4A, H).

Twenty-nine individual lingulids occur beneath the *Rafinesquina* or other objects in the 26 thin sections from the vertical valve serial set (Fig. 4; not all thin sections illustrated). The horizontal serial set (Fig. 5; not all thin sections illustrated) contains sixteen separate lingulids in 30 sections, all clustered beneath *Rafinesquina* valves, and all intact and spar filled. Thirty spar-filled lingulids occur in the 37 thin sections of the vertical bed serial set (Fig. 6; not all thin sections illustrated).

Morphology of the Burrows

On polished slabs cut horizontally through the packstone to siltstone transition (Fig. 3), as well as in thin section (Figs. 4–6), burrows show both vertical and horizontal orientations. Cross sections of burrows that are oriented horizontally are elliptical. At least as many horizontal segments as vertical ones are present, and vertical burrows are rarely traced through more than a few thin sections in any of the serial sets. A light, sediment- or spar-filled tubular feature bisects many of the burrows in cross-section (Fig. 3C). The structure of these burrows exhibits the morphology of the lingulid escape trace *Lingulichnus hamatus* Zonneveld and Pemberton (2003) in having a central pedicle trace (Pt on Fig. 3C) within a larger, curved, circular to elliptical tube. The pedicle trace is the tubular cavity left by passage of the pedicle that has subsequently filled in with finer sediment or diagenetic cement.

The type species of *Lingulichnus*, *L. verticalis* (Hakes, 1976), a dwelling trace, commonly exhibits concentric laminae or spreiten (Zonneveld and Pemberton, 2003). These features, if present, are faint in *L. hamatus*, due to the speed with which the burrow was created. The Ordovician specimens discussed herein lack such laminae as well, although shell fragments within the burrows are sometimes arranged in a roughly concentric fashion (Fig. 5S).

Burrows within the lower parts of the bed more often display the characteristic morphology of *Lingulichnus hamatus* (Figs. 5A–K) in having a distinct pedicle trace. Burrows are also present in the upper sections from this series of sections, but just below the uppermost *Rafinesquina*, individual burrows become difficult to distinguish (Figs. 5Q, R). Perhaps as the brachiopods became trapped they attempted to burrow in different directions, trying to find their way upward. As they clustered together, their burrows merged and are less distinct. Spar-filled pedicle traces can sometimes be seen just below the *in situ* lingulids (Fig. 4G), where a void was left as tissue decayed.

In thin section, burrows are mostly filled with muddy silt with some small shell fragments, contrasting with the densely packed shell material in the surrounding sediment (Figs. 4B–C). In the thin sections of the vertical valve serial sets, short segments of vertical burrows are present beneath some of the lingulids, and in many cases, lingulids are observed at the top of their burrows (Figs. 4B–C).

In the lower thin sections of the horizontal serial set, a burrow that initially appeared to be an unusually wide burrow (Fig. 5A) proved to be two adjacent burrows, each with a darker pedicle trace visible. This distinctive feature is even more obvious in the overlying section (Fig. 5B) where the two burrows begin to diverge. In the next few sections above (Figs. 5C–K), the two burrows diverge further as one lingulid continued to take an upward path and the other burrowed more horizontally. Although subsequent compaction may have enhanced the sinuous nature of the burrows, it is clear that these brachiopods deflected their burrows around obstacles.

Orientation of Burrows in Relation to Shell Debris

In several instances, the burrows can be traced around specific obstacles. In Figures 5I–K, a burrow deflects around an unknown round object in the lower left of the section. In Figure 5L, two burrows encounter a ramose bryozoan. One burrow deflects to the left and one to the right. The two burrows and the bryozoan can be traced for 5 mm, through 5 serial sections (Figs. 5L–P). The pedicle trace is also visible on the right burrow (Figs. 5N, S).

The majority of the lingulids are trapped beneath *Rafinesquina* shells in the upper part of the bed. However, some lingulids were trapped beneath shells of other taxa in the same bed. Thin sections from the vertical bed serial set show two lingulids trapped at the end of their burrows beneath a calcite-replaced fossil, likely a bivalve (Figs. 6A–B). Another thin section from the same set (Fig. 6C) appears to show lingulid burrows oriented horizontally beneath another bivalve shell. There are also instances of lingulids trapped beneath other, lower shells (Fig. 6C). In many places the *Rafinesquina* shells are stacked and in several cases, the lingulids appear to have burrowed upward beneath one *Rafinesquina* shell only to end up trapped between two shells (Figs. 6D–F). The distinctive oval cross section and lighter-colored pedicle trace of *Lingulichnus* is seen through several sections (Figs. 6D–E) terminating at the lingulid shell (Fig. 6F).

In some cases, multiple lingulids followed a similar path upward. In one section (Fig. 4C) a cluster of lingulids occurs at the top and to the right of a wide burrow that in the adjacent thin section proves to be two burrows (Figs. 4B, G), each with a lingulid *in situ* at its top. The left specimen appears in cross-section to be in burrowing-upward position, with the blunter posterior end downward. A spar-filled area just below the posterior end marks the cavity left as the pedicle decayed. The anterior tip of the shell rests just beneath a small overlying obstacle, revealing that the brachiopod was burrowing upward and died at the top of its burrow after encountering this small obstacle. The burrow to the left has four lingulids at its end, all in a row just beneath the *Rafinesquina*. Three have flattened out against the overlying obstacle, but the last one, trapped behind the others, was not able to do so fully. Three lingulids form another cluster situated directly under the highest part of the *Rafinesquina* (Figs. 4B–F). They also appear to have burrowed upward along a similar route from a different direction. Yet another lingulid (Fig. 4B, center) took a different route upward and ended up trapped beneath an impenetrable stack of shell fragments.

IDENTITY OF THE LINGULID

Based mostly on characteristics of the hinge line, these lingulid specimens are tentatively identified as cf. *Pseudolingula*, although the internal features of the type species and other species of the genus (Holmer, 1990) are not seen on these minute brachiopods. Several species of the genus have been reported previously from similar strata.

Pseudolingula cincinnatiensis (Hall and Whitfield, 1875) was reported from Fairview strata (Dalvé, 1948) although the original type locality information is vague. *Pseudolingula covingtonensis* was identified from the Cynthiana formation, now reassigned to the Point Pleasant and lower Kope formations, although the original type locality is quite vague (Foerste, 1916). The type specimen of *P. covingtonensis* is 12.6 mm long and 10 mm wide (Foerste, 1910). No measurements for *P. cincinnatiensis* were given and no scale accompanies the illustrations, but it was described being above the medium size, while *P. covingtonensis* was described as rather below the medium size (Hall and Whitfield, 1875, p. 67). The specimens considered herein are generally less than half a centimeter in maximum dimension. Although most lingulid specimens are too embedded in matrix to measure precisely, the large population appears rather uniform in size. The many growth lines and small size of the larval shell relative to the rest of the valve (Fig. 7A) suggest these were mature brachiopods rather than a spatfall of juveniles. The interiors of *P. cincinnatiensis* and *P. covingtonensis* are poorly known and not easily compared to the material discussed herein. The lingulids described herein do appear to lack a median septum on both valves, a feature preserved in *P. cincinnatiensis* (Hall and Whitfield, 1875). Kramer (1972) assigned three previously described Cincinnatian species to *Pseudolingula* and described a new species as well, but none matches these specimens in morphology or size range.

The most distinctive feature seen on etched specimens is a knob at the dorsal beak (Figs. 7D–F). This feature has not been described for any Cincinnatian *Pseudolingula* species, although none of these species were described from etched material. The distinctive knob is not observed on non-etched specimens. It is possible that these specimens represent a previously unreported species of Cincinnatian lingulid.

INTERPRETATIONS

Storm Burial of Lingulids

The concentration of cf. *Pseudolingula* beneath the *Rafinesquina* valves and the general absence of cf. *Pseudolingula* in the surrounding sediment rule out a random association. The lack of articulated *Rafinesquina* valves indicates that the association occurred after the death of the *Rafinesquina*. The lingulids appear to have become trapped under *Rafinesquina* shells as they attempted to escape burial by burrowing upward through newly redeposited sediment, including the *Rafinesquina*-dominated shell bed (Supplementary Data 4–5[1]).

The exceptional preservation of the lingulids indicates that they were not transported from another location during the storm. The concentration of *Rafinesquina* near the top of the packstone is the result of winnowing and reworking by a storm, which also explains the nearly uniform concave-downward orientation of the *Rafinesquina* shells (e.g., Kreisa and Bambach, 1982). The lack of size sorting of *Rafinesquina* shells and fragments suggests that these shells were not transported from elsewhere (e.g., Lever and Thijssen, 1968; Trewin and Welsh, 1972). This lack of significant transport is also supported by observations that meter-scale lateral variation in fossil distribution in other Cincinnatian strata is generally preserved, even in beds that have been disturbed by storms (Miller, 1997; Barbour, 2001; Webber, 2005), and by the shear mass and lateral extent of Cincinnatian shell beds, for which there is no plausible source area (Brett et al., 2008). The abundance of both lingulids and *Rafinesquina* shells in this bed also suggests that their association after the storm mirrors a pre-storm assemblage.

Lingulid Escape Behavior

Burrowing.—*Pseudolingula* has previously been interpreted as an infaunal filter feeder (Frey, 1987; Lehman and Pope, 1989). *Pseudolingula* also exhibits morphology (Figs. 4H, 7) generally associated with burrowing, such as a reduced brachial pseudointerarea and smooth, elongate, suboval valves (Emig, 1997; Bassett et al., 1999). Survival in a mobile substrate necessitates the capability to reorient. Individuals may be buried, exhumed, or both during storm events (Zonneveld and Greene, 2010). Modern lingulids can escape burial by moving upward in the sediment, whether buried *in situ* or exhumed on the seafloor before reburial in sediment (Paine, 1963; Thayer and Steele-Petrović, 1975; Emig, 1983; Hammond, 1983). Reburrowing after exhumation by modern *Glottidia pyramidata* is accomplished through a combination of valve movement and sediment clearing by setae (Thayer and Steele-Petrović, 1975). In experiments performed by Thayer and Steele-Petrović (1975), both brachiopods in established burrows and exhumed specimens were covered with various amounts of sediment. Both groups were able to successfully reorient themselves relative to the sediment-water interface. Although the pedicle plays a role as a muscular prop in reorienting an exhumed lingulid brachiopod into a digging-downward position, the pedicle is not used as a mechanism for burrowing (Thayer and Steele-Petrović, 1975). Modern lingulids may lose their pedicle during exhumation and transport (Hammond, 1983), but are still able to burrow upward after burial (Hammond, 1983; Emig, 1983).

The lingulid escape trace *Lingulichnus hamatus*, with its distinctive pedicle trace, is abundant in this bed and can be seen clearly in both horizontal and vertical cross-section. In one vertical section of *L. hamatus*, many of the small shell fragments seen within the burrow (Fig. 6G) are rotated about 45° relative to similarly shaped fragments in the bed. To the right of the burrow, they are oriented with the uppermost end away from the burrow and lowermost end toward the burrow and on the left side of the burrow, the orientation is the opposite. This fragment orientation is suggestive of the way lingulid brachiopods burrow, using their setae and shell movements to pass cleared sediment around their shells to the posterior as the pedicle (if present) trailed behind. These lingulids were buried by sediment during a storm and began burrowing upward to escape.

Initial Survival Rate.—The three illustrated series of thin sections (Figs. 4–6) allowed observation of 75 articulated, spar-filled lingulids. All of the specimens trapped beneath various obstacles are either in upward-burrowing position, with the blunter posterior end down and anterior end up (Figs. 4B, G), or they have flattened out horizontally against the overlying obstacle, with their anterior end pointing in the direction of the highest point beneath the obstacle (Figs. 4B–G). Thus, all specimens are interpreted to have been alive after the storm and moved to their final position at the end of their own burrow. This high exhumation and reburial survival rate indicates that if they were transported at all, it was likely quite minimally. This rate of storm survival is much higher than that reported for Middle Triassic in British Columbia (Zonneveld and Greene, 2010). In that study, the lowest rate of storm mortality reported was 10%, although many individual beds studied had a much higher rate. One explanation for the high initial survival rate observed in this Ordovician occurrence is that the lingulids were not actually transported, but remained in their burrows as shelly debris was deposited on top of them. In this case, the distinctive dwelling trace *Lingulichnus verticalis*, with its vertical spreiten indicating backfilling, should be present in the underlying sediment, but is not. Another explanation for the high rate of transport survival is that these lingulids were so tiny that the viscosity of water may have offered them some protection against damage. The Middle Triassic lingulids from British Columbia (Zonneveld and Greene, 2010) were significantly larger and perhaps more easily damaged. This disparity is in agreement with differing amounts of damage seen on modern clams after storms, where larger clams are more likely to be damaged by chipping during collisions in transport than smaller ones (Boyajian and Thayer, 1995).

Obstacles.—The U-shaped *Lingulichnus hamatus* burrows were interpreted by Zonneveld and Pemberton (2003) as lingulids re-burrowing after exhumation by a storm. The J-shaped burrows were interpreted as individuals reestablishing themselves after burial during the same storm event. These burrows were described in a variety of siliciclastic sediments of the Triassic Montney and Liard formations of western Canada. The loose silt and sand would have offered little impediment to upward progress for these brachiopods.

In contrast, the shell-filled sediments of the Fairview Formation provided a complex obstacle course for an upward-burrowing brachiopod. These Ordovician burrows are not clearly J-shaped, but instead appear to be deflected frequently as the brachiopod encountered obstacles to upward progress (Figs. 5L–P). The lingulids burrowed upward when possible but, upon hitting an obstacle, often had to burrow horizontally until vertical escape was again possible (Figs. 5D–F, H–K).

Merged burrows are numerous in these thin sections, as are instances of diverging burrows. If many lingulids are deflecting around the same obstacles it is to be expected that their burrows might often merge. In several cases, the lingulids occur in rows at the top of a single burrow (Figs. 4B–G). As burrows merged, brachiopods were funneled together and trapped in clusters and rows at the ends of their burrows. Following the route of another brachiopod upward might also ensure easier burrowing through looser, less debris-filled sediment.

Although the lingulids were clearly very efficient at burrowing upward, they commonly became trapped beneath obstacles on their way up. The majority of the victims are clustered beneath large objects, primarily *Rafinesquina*, but also beneath possible bivalve shells (Figs. 6A–C). One lingulid (Fig. 4B) became trapped beneath a relatively small object that is no larger than many of the other obstacles that were bypassed by lingulids on their way up. This specimen is preserved in life burrowing-upward position. Perhaps it was exhausted from the effort of attempting to escape and unable to make the effort to deflect around the obstacle. Modern *Lingula* buried experimentally under 20 cm of sediment burrowed upward, but in some cases died before reaching the surface (Hammond, 1983).

The largest lingulid observed in thin section is also the lowest individual trapped. Figure 6H shows six lingulids, five of which are trapped beneath the upper layer of *Rafinesquina* shells. These five lingulids are similar in size to each other and to other lingulids observed in a similar position on other slides. The sixth individual is significantly larger than the others. A portion of its burrow, and possibly its spar-filled pedicle trace, are located to the right of the specimen indicating that it was buried alive, and made an attempt to escape but was trapped before it made significant upward progress. This observation may suggest that there was a screening effect in which larger individuals were more likely to become trapped as they attempted to burrow upward, and some smaller lingulids were able to utilize smaller openings between shell fragments. Large individuals are also heavier, and may have settled out of the water column sooner than smaller ones, thus becoming trapped in the lower layers of the storm deposit. A similar pattern of a higher mortality rate of larger bivalves catastrophically buried in sediment is seen in the modern environment (Peterson, 1985).

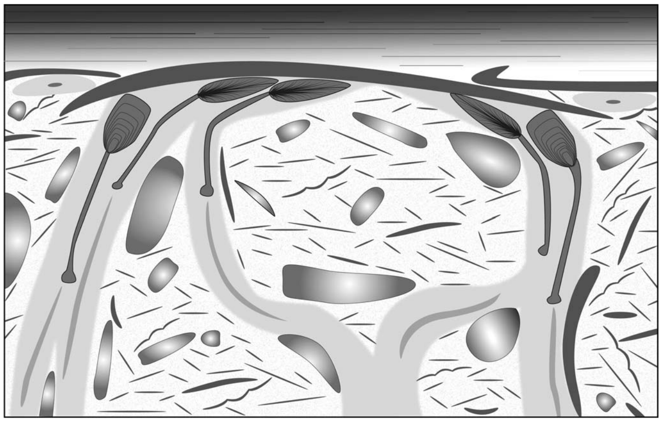

FIGURE 8—Generalized representation of occurrence of lingulids trapped beneath *Rafinesquina* shell bed. Five lingulids burrow upward, deflecting around the same obstacles until their burrows merge and they find themselves trapped beneath a *Rafinesquina* shell. To the far right and left a lingulid has become trapped by a *Rafinesquina* shell and burrowed horizontally, leaving behind the trace fossil *Lingulichnus hamatus.*

DISCUSSION

Burrows interpreted as fugichnia are generally straight and oriented vertically upward. Examples include the lingulid escape trace *Lingulichnus hamatus* (after reestablishment of upright position; Zonneveld and Pemberton, 2003; Zonneveld and Greene, 2010) and sedimentary structures interpreted as unnamed escape burrows (e.g., Kreisa, 1981). The material discussed herein differs in that the route upward was frequently interrupted by shelly obstacles. Upward-burrowing lingulids needed to deflect by burrowing laterally until a way up was available. If the lingulid encountered a ramose trepostome bryozoan (Figs. 5L–P), a gastropod, or an articulated biconvex brachiopod, it could easily deflect around the obstacle, the contours of which guided the lingulid in a path that continued upward (Fig. 8). If the lingulid encountered a concave-downward *Rafinesquina* shell or other concave object, it would have needed to make a sharp 90°+ turn in its burrow to escape. It is more likely that the instinct for upward movement would instead guide the lingulid toward the highest point beneath the overlying shell before upward progress ceased altogether (Fig. 8). This behavior is consistent with the observed clusters of lingulids beneath the centers of the *Rafinesquina* shells. In only one instance (Fig. 4B) in all of the sections examined, did the lingulid get trapped beneath anything other than a concave-downward obstacle, or combination of obstacles. The "Curse of *Rafinesquina*" may thus lie in its orientation.

Escape burrowing of infaunal, suspension-feeding organisms involves an instinct to go upward toward the sediment-water interface (Shäfer, 1962; Maurer, 1967; Kranz, 1974; Schulenberger, 1970; Nichols et al., 1978; Maurer et al., 1986). Apparently, lingulids in the study interval were either incapable of downward burrowing or lacked the instinct or cognitive capacity to burrow around a concave-downward obstruction and were thus stranded below the center of individual *Rafinesquina* shells. Data on the ability of modern lingulid brachiopods to navigate shelly substrata are lacking and thus it remains unclear if lingulids have ever evolved this ability.

The majority of burrows end beneath *Rafinesquina*, but there are gaps in places between the *Rafinesquina* shells where lingulids presumably could have escaped. Some possible successful escape burrows are visible in the large horizontally oriented slabs above the *Rafinesquina* layer (Figs. 3B–D), but these may have been individuals that were entombed in the upper sediment layer and thus did not need to navigate the *Rafinesquina* barrier.

The association of lingulids beneath *Rafinesquina* shells has not been reported from Cincinnatian strata previously. Recent collecting has yielded similar specimens from similar strata at nearby outcrops, although not in the large numbers seen at the study locality. Further analysis and careful collecting are needed to establish if this phenomenon is more widespread than is indicated by analyses to date.

Lingulid-Strophomenid Association

Shell beds in general are commonly considered to comprise time-averaged assemblages (e.g., Kidwell and Boscence, 1991; Kowalewski et al., 1998). Storm events are assumed to have a negative taphonomic effect for most organisms present at the time of the storm (e.g., Kreisa and Bambach, 1982). However, in the present study area, storm burial contributed to the preservation of an unusual association of lingulid and strophomenid brachiopods. Taphonomic conditions provided by the final storm event, including burial under a layer of muddy siltstone, preserved an association between dead, disarticulated *Rafinesquina* shells and live, articulated lingulids. The *Rafinesquina* pavement protected the lingulid valves from subsequent reworking and from infaunal scavengers, and the deposition of the siltstone sealed the association away permanently. The only disturbance to the lingulid valves subsequently was limited separation and rotation of the valves, perhaps as gas was released during decay. The rapid burial of skeletons with intact tissues, especially in voids beneath overlying shells, may have led to early mineralization (e.g., Brett and Baird, 1986; Brett et al., 2012). These lingulid shells are lined with pyrite, a mineral that commonly forms in the presence of decaying organic matter (Brett and Baird, 1986; Canfield and Raiswell, 1991). It thus appears that decay of the trapped lingulids apparently contributed to their own unusual preservation. Lingulid valves are organophosphatic, and modern lingulids do not have a high preservation potential (Emig, 1990; Kowalewski, 1996). Although the lingulids were likely a long-term component of this shallow-shelf community for some time, close examination of bioclastic detritus in this bed reveals no other evidence of their presence. It is thus presumed that the same obrution event that destroyed the community provided the unique biogenic and diagenetic signature that preserved this unique association.

Lingulids in Carbonate Shell Gravel

This occurrence of Ordovician lingulids inhabiting carbonate shell gravel is unusual, given the modern and fossil distribution of lingulids. Modern lingulids are rare in carbonate sediments (Paine, 1970; Thayer and Steele-Petrović, 1975). Paine (1970) also reports that modern lingulids do not inhabit gravel bottoms at all. The extant lingulids *Lingula* and *Glottidia* live primarily in sand and silt-sized siliciclastic sediment (Paine, 1963, 1970), and occur in both intertidal and subtidal environments (Emig, 1983, 1997). Other reported occurrences of Ordovician *Pseudolingula* (Wilcox and Lockley, 1981; Lehman and Pope, 1989; Candela and Hansen, 2010) have a distribution within the range of their modern counterparts (Paine, 1963, 1970). Lehman and Pope (1989) report the genus as part of a low-diversity fauna preserved in fine siliciclastic sediments from the Upper Ordovician of Pennsylvania. Species of *Pseudolingula* from the Middle Ordovician of Norway lived in low-energy fine siliciclastic sediments deposited near apparent storm wave base (Candela and Hansen, 2010). A Middle to Late Ordovician (Llandeilo Series) *Pseudolingula* from Wales occurs in siliciclastic sediment deposited just above apparent storm wave base (Wilcox and Lockley, 1981). All of these occurrences are consistent with the siliciclastic habitats of modern lingulids (Paine, 1970).

Modern genera (as well as other Ordovician species of *Pseudolingula*) are much larger than these specimens, and perhaps their preference for a siliciclastic substrate is partially controlled by the ease of burrowing out of such a substrate after a storm and the lowered likelihood of encountering obstacles on the way upward. These small cf. *Pseudo-*

lingula sp. may have been better adapted to maneuverability in a shell-filled environment. Their small size also means that they may have been able to inhabit pockets of finer-grained siliciclastic sediment that accumulated between shells. Given that the storm winnowed the mud and silt that became part of the upper muddy siltstone component from the shells that became part of the lower shelly packstone component, it is likely that the lingulids were established in pre-storm sediments that included a higher percentage of fine siliciclastic sediments and sand-sized shell fragments than the shell-rich layer in which the lingulids were entombed; winnowing might have smeared decimeter-scale shell-rich sediment patches laterally, and the postevent settling process obviously reordered materials by settling velocity. However, given the abundance of large shell fragments within the bed and the vast numbers of lingulids present, the lingulids must have been at least somewhat tolerant of carbonate shell gravels.

Negative Taphonomic Feedback and Ecosystem Engineering

Rafinesquina was adapted to dwelling upon soft substrates (Thayer, 1975; Dattilo et al., 2009; Plotnick et al., 2011). Brachiopods with thin, flat valves were often pioneer species in newly deposited soft sediments (Walker and Alberstadt, 1975; Harris and Martin, 1979). The accumulation of *Rafinesquina* shells enhances the recruitment of epibenthic species, some of which colonize the shells of living *Rafinesquina* and others, subsequently their dead shells (e.g., Meyer, 1990). In this way, *Rafinesquina* served as an inadvertent autogenic ecosystem engineer (Jones et al., 1994), both while living and eventually, through taphonomic feedback (Kidwell and Jablonski, 1983; Kidwell, 1986a, 1986b), in the interaction of live organisms with dead shells.

For the epibenthos, the accumulation of *Rafinesquina* shell debris was likely a positive phenomenon; however, it was not likely conducive to the development of an endobenthic community. Kidwell and Jablonski (1983) suggested that the accumulation of shells may eventually exclude larger infauna. Bouma et al. (2009) predict that as the primary autogenic structures of the epibenthos (dead or alive) become more developed and diverse, this increased diversity is at the expense of diversity within the endobenthos. In the terminology of Bouma et al. (2009), the structures produced by the epibenthos play the role of ecosystem engineering exclusion. This interaction has not been documented in the fossil record, nor is it well documented in modern environments. Dense roots of cordgrass exclude burrowing lugworms in some intertidal sediment, while the burrowing of lugworms in other intertidal sediments make it impossible for cordgrass to establish (Van Wesenbeeck et al., 2007). Peterson and André (1980) demonstrated experimentally that the growth of one infaunal bivalve was impeded by the presence of the dead shells of two other bivalves placed in the sediment. In this case, all of the bivalves were infaunal, but it does illustrate a similar form of negative taphonomic feedback to that hypothesized by Kidwell and Jablonski (1983).

In most cases of ecosystem engineering exclusion or negative taphonomic feedback (documented, experimental, or hypothetical), the presence of one organism negatively impacts the routine behavior of another. The association between *Rafinesquina* and a lingulid brachiopod in the study area may suggest another possibility: that the presence of one organism may be apparently neutral in some circumstances but detrimental in others (i.e., after storm concentration of shell material). If we consider an ecosystem an association of living organisms and their physical and chemical surroundings, then the storm-deposited sediment constituted a new ecosystem in which dead shells played an exclusionary role as the lingulids attempted to re-establish themselves. The storm was the primary cause of sudden deleterious conditions for organisms that survived it, but it was the presence of the *Rafinesquina* shells that impeded the successful escape of the lingulids.

Ecosystem engineering has been recognized to play a positive role in increasing biodiversity through the Phanerozoic (Erwin, 2008). Minimal attention has been paid to the evolutionary role of negative ecosystem engineering, especially through the history of the interactions between the marine epifauna and infauna. Further research is required to establish whether the evolution of large flat brachiopods, like the strophomenids, influenced the distribution of infaunal organisms such as lingulids. Did negative taphonomic feedback that occurred during exceptional, albeit geologically frequent, events play any role in changing ecologic relationships or community structure through time? Is the Curse of *Rafinesquina* an isolated event of minor significance, or was it a factor in the evolution of the Paleozoic marine environment?

CONCLUSIONS

1. The clusters of *Pseudolingul*a beneath *Rafinesquina* and their associated burrows demonstrate that lingulid brachiopods have long had the ability to burrow upward and re-establish themselves after burial during a storm event, even though these particular lingulid brachiopods were unfortunate enough to encounter a physical barrier to their upward progress. The large number of *Pseudolingula* trapped beneath *Rafinesquina* also indicates that this Ordovician lingulid brachiopod was not only capable of burrowing upward after burial but was very effective at doing so. This finding demonstrates that the instinct for upward burrowing after burial during a storm had evolved in lingulid brachiopods by the early Paleozoic.
2. Ordovician lingulid brachiopods were more diverse in their habitats than living lingulids. The lingulids documented herein were tolerant of living in a carbonate shell gravel-dominated environment, one that would exclude modern lingulids. Small size may have played a role in their ability to persist in pockets of siliciclastic sediment among large shells and shell fragments.
3. This association also indicates that the formation of a storm-deposited shell pavement of downward-concave *Rafinesquina* greatly inhibited the ability of the lingulids to escape burial. The role of *Rafinesquina* as an ecological engineer is apparently more complex than has been previously realized, and this association documents a previously unconsidered form of both negative taphonomy and ecosystem engineering exclusion: the interactions between dead shells and live organisms during exceptional events that cause sudden changes to the ecosystem.

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