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TAPHONOMIC BIAS OF SELECTIVE SILICIFICATION REVEALED BY PAIRED PETROGRAPHIC AND INSOLUBLE RESIDUE ANALYSIS

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ABSTRACT: Silicification is an important mode of fossil preservation but the extent to which silicified material represents an unbiased sampling of the total fossil assemblage within a given rock sample remains poorly quantified. Here, we use paired analyses of thin sections and acid-extracted silicified specimens from the same samples to examine the biases introduced during silicification of Lower Triassic Virgin Limestone carbonates preserved in the Muddy Mountains of southern Nevada. Bivalves dominate most thin sections in the point count data, but rarely silicify completely enough to be recognized in residue. Echinoderms and gastropods are less abundant in thin section but dominate the residues. The abundances of these groups in thin section and residue are only weakly correlated. These findings suggest that although silicification generally captures relative trends in proportional abundance of higher taxa among samples, the silicification process can be taxonomically biased. Given the biases that can occur during silicification, it should not be assumed that silicified collections present a pristine picture of taxonomic or paleoecologic composition. Petrographic analysis has the potential to illuminate the reliability of paleontological data based on silicified collections.

INTRODUCTION

Silicification is an important mode of fossilization that often appears to preserve a more complete record of higher taxa than some other modes of preservation (e.g., Schubert et al. 1997; Cherns and Wright 2000; Kidder and Erwin 2001; Butts and Briggs 2010). Consequently, silicified faunas can serve as an important control on taphonomic losses under more conventional circumstances (e.g., Cherns and Wright 2000; Clapham and Bottjer 2007). Because silicified fossils are typically extracted from carbonate strata via dissolution of the carbonate matrix and the vast majority of marine invertebrate fossils are composed of calcium carbonate, the non-silicified component of these samples is typically lost without study. In rare cases, beds with very early and pervasive silicification preserve high fidelity fauna, and the loss of fauna is demonstrated by comparison with nearby less pervasively silicified faunas (Cherns and Wright 2000, Wright et al. 2003). Nevertheless, the extent to which silicification itself is biased in terms of the size, mineralogy, or taxonomic affinities of the fossils that it preserves within a given stratum has not been quantified (e.g., Cherns and Wright 2000; Butts and Briggs 2010; Butts 2014). Understanding these biases is critical to the paleoecological interpretation of silicified fossil assemblages.

The Lower Triassic Virgin Limestone Member of the Moenkopi Formation, whose silicified faunas have been previously documented (Boyd and Newell 1997; Moffat and Bottjer 1999), presents an ideal opportunity to assess the extent to which silicification is itself biased. In this study, we present data on the faunal composition of the Virgin Limestone gathered by two methods: individual counts of silicified shells produced through acid maceration of limestone and point counting of thin sections made from the same rock samples. Paleoecological studies of the Early Triassic have been based on both silicified and non-silicified assemblages (e.g., Schubert and Bottjer 1995; Payne et al. 2006; Wheeley and Twitchett 2005), and understanding the role of bias is essential in

understanding paleoecology at this and other critical intervals in Earth history.

GEOLOGIC SETTING AND METHODS

The Virgin Limestone Member of the Moenkopi Formation crops out in present-day Nevada, Utah, and eastern California and consists primarily of fossiliferous limestone interbedded with siltstone and rare sandstone. Deposition occurred in a mostly subtidal setting along the shallow, epicontinental shelf of a passive margin. Age constraints provided by ammonoids (Poborski 1954) place the Virgin Limestone in the Spathian Stage, which is uppermost Lower Triassic. For this work, we collected samples at the Ute and Overton localities in the Muddy Mountains of southern Nevada.

We collected 24 fossiliferous packstone and grainstone samples from carbonate beds that exhibited silicification within the Ute and Overton outcrops (Fig. 1; Shorb 1983; Pruss et al. 2005) but only 11 of these samples yielded abundant and well preserved fossils in residue. From each sample, we dissolved ~ 140–260 g of rock in ~ 200–400 mL 10% glacial acetic acid solution buffered with ammonium acetate to isolate silicified material (method modified from Jeppsson et al. 1999; Dalton et al. 2013); some dolomitized fossils were also extracted but these were far less abundant than silicified specimens. Samples were kept in acid for two to three months until at least 50% of the rock had dissolved. Residues were wet-sieved and all grains in the three largest size fractions (> 3.35 mm, 3.35–0.853 mm, and 0.853–0.500 mm) were sorted by hand into fossil and non-fossil material (e.g., silicified ooids and intraclasts, insoluble minerals such as pyrite). The most abundant fossiliferous size fractions were 3.35–0.853 mm and 0.853–0.500 mm. Fossil material was further identified as bivalve, gastropod, crinoid, brachiopod, echinoid or unidentified fossil fragments, and the number of grains (whole shells and shell fragments combined) in each taxon was counted. For three samples that produced

TABLE 1.—Point count and residue data from the eleven samples that were compared. Totals are given, and the percentages (in parentheses) express the portion of the sample made up of each taxon.

Sample number	Analysis	Bivalve	Gastropod	Echinoderm	Un-ID or other
SVU12-30	thin section	22 (76%)	0	0	7 (24%)
	residue	8 (13%)	35 (58%)	0	17 (28%)
SVU12-33	thin section	91 (88%)	0	13 (13%)	0
	residue	7 (17%)	1 (2%)	33 (79%)	1 (2%)
SVU12-41A	thin section	15 (60%)	0	9 (36%)	1 (4%)
	residue	6 (9%)	1 (2%)	57 (89%)	0
SVMM12-38	thin section	33 (51%)	3 (5%)	12 (18%)	17 (26%)
	residue	20 (11%)	98 (54%)	16 (9%)	46 (26%)
SVMM12-40	thin section	12 (50%)	2 (8%)	0	10 (42%)
	residue	2 (50%)	2 (50%)	0	0
SVMM12-46A	thin section	47 (92%)	0	0	4 (8%)
	residue	461 (84%)	68 (13%)	1 (0%)	15 (3%)
SVMM12-46B	thin section	24 (42%)	1 (2%)	22 (39%)	10 (18%)
	residue	0	147 (47%)	140 (45%)	26 (8%)
SVMM12-46 C	thin section	33 (54%)	0	0	28 (46%)
	residue	128 (96%)	0	6 (4%)	0
SVMM12-48A	thin section	55 (67%)	2 (2%)	18 (22%)	7 (9%)
	residue	5 (0%)	0	1507 (99%)	3 (0%)
SVMM12-48B	thin section	9 (75%)	0	0	3 (25%)
	residue	30 (100%)	0	0	0
SVMM12-48C	thin section	47 (57%)	0	31 (38%)	4 (5%)
	residue	1 (0%)	0	220 (94%)	14 (6%)

exceptionally large residues (SVMM12-40, SVMM12-46C and SVMM12-48C) only 25–50% of the residue was sorted and counted as the goal here was to ascertain dominant components of each residue; for all others 100% of residues were counted. Fragments were counted if they could be satisfactorily identified. A subset of well-preserved fossils in residue was imaged under the Scanning Electron Microscope (SEM) using an FEI Quanta 450 Scanning Electron Microscope at the Center for Biological Microscopy at Smith College.

The same hand samples from which the residues were derived were thin-sectioned, and ~200 points on each slide were identified and counted according to the grain-solid method (e.g., Van der Plass and Tobi 1965; Flügel 2004; Payne et al. 2006; Pruss and Clemente 2011). For this purpose we used a petrographic microscope (Olympus BH-2) rigged with a mechanical stage to move the slide at 0.5 mm intervals. All carbonate phases were counted and quantified in thin section but since fossiliferous packstone and grainstone were analyzed in this study, fossils were well represented in the counts.

RESULTS

We counted and identified 3,123 fossil shells and shell fragments in the silicified residues. Bivalves, crinoids, and gastropods dominate the residues, accompanied by rare echinoid spines and some unidentified fossil material (Table 1). We identified 122 grains as fossil material by their texture or shape but were unable to classify them further. Crinoid fossils typically occur as isolated ossicles, although fragments containing two or three columnals occur occasionally. In two residues, echinoid plates and spines occur in size fractions smaller than the ones that we counted, suggesting that the overall proportion of echinoderms in residue (at least in those samples) could be higher. In general, when crinoids were abundant, crinoid fragments dominated the largest size fractions but were much less common among the smaller size grains.

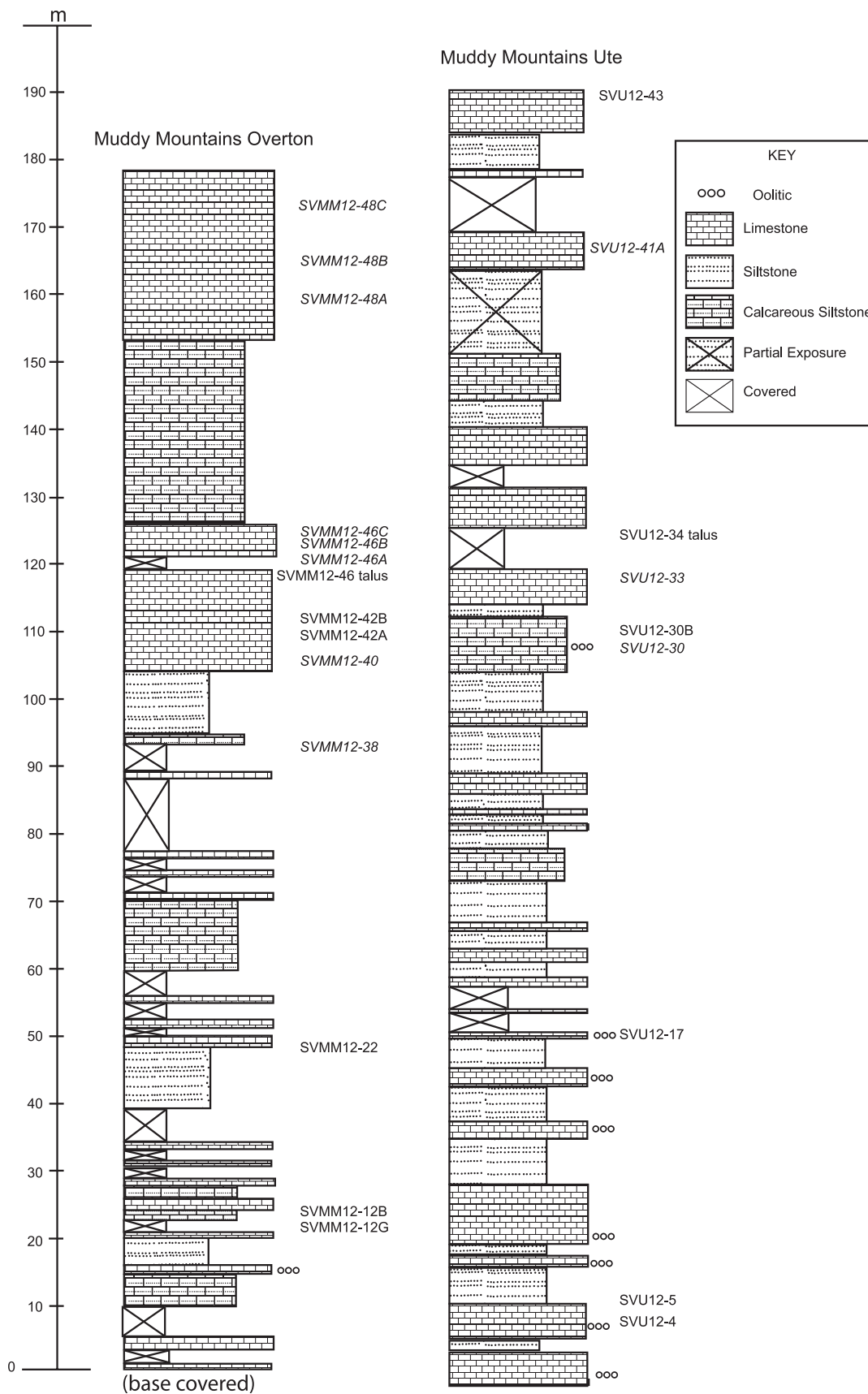
Fossil material accounts for 25% of the points counted in petrographic analysis of the 11 slides. Of all of the fossils counted in thin section, silicified specimens make up less than 5% of these points in thin section and were generally not abundant. Crinoids, bivalves and gastropods occur abundantly in residue and thin sections. Rhynchonelliform brachiopods, lingulids, serpulids and ostracodes are present in thin

sections at low frequencies (<2%) but are rare or absent in residues. Foraminifera also occur in thin section but are sufficiently rare that they were never among the points counted in the quantitative compositional analysis. Sixty-two points were identified as fossil material but could not be assigned taxonomically even at the phylum level. Echinoid plates and spines were more prevalent in thin section than in the residues, but because crinoid and echinoid plates can be difficult to distinguish petrographically, we grouped them together in point counts.

Across samples, the abundance of a given taxon measured by point counts is positively correlated with its abundance measured by specimen counts of silicified material extracted from acid residue (Fig. 2). The positive association is statistically significant for echinoderms (Pearson's $\rho=0.77$, $p=0.003$) and marginally so for bivalves ($\rho=0.54$, $p=0.05$) and gastropods ($\rho=0.57$, $p=0.05$). Rank-order correlation (Spearman's rho) yield comparable results. Thus, both silicified residues and point counts capture information regarding the samples in which each taxon is comparatively more or less abundant.

However, there is also substantial bias in the representation of different clades in silicified material versus bulk rock analysis via point counting (Figs. 2, 3). Generally, gastropods and echinoderms are disproportionately more abundant in residue than in thin section. In fact, gastropods are only a minor component in thin sections but an important fraction of the material in residues. In contrast, bivalves are abundant in point count analyses but typically less abundant in residue. In the three samples in which bivalves are abundant in both, bivalves make up the most points in thin section with unidentified fossils making up much of the remaining points (Table 1). In SVMM12-46C, for example, almost all identifiable fossils in both thin section and residue are bivalves, and likewise in SVU12-30 (with no echinoderms in either residue or thin section) and SVMM12-48B. The rest of the samples show greater variation between analyses (Table 1). Sample SVMM12-46B contained echinoderms in both residue and thin section, but the residue also contained only gastropods (see Table 1) whereas bivalves dominate point counts in thin section. A similar pattern occurs in SVMM12-38, but the large proportion of unidentified residue material makes it less clear-cut. In SVMM12-46A, 68 (13%) gastropods appear in residue without a single corresponding gastropod in point counts; high numbers of bivalves are present in both, however (Table 1).

Virgin Limestone Member



Petrographic inspection and SEM imaging of fossil grains provide some insight into the differences between fossil abundances in bulk rock versus residues (Fig. 4). For example, crinoids are often the only silicified taxon in a single thin section, even when fossils of other types are adjacent to them (Fig. 4B, 4C), although not all crinoids are silicified in thin section. SEM examination reveals silica cement with spongy or granular texture (e.g., Butts and Briggs 2010) and hollow interiors of many ossicles. Bivalves are typically thin and elongate in thin section and partially silicified (Fig. 4D–F); they are abundantly silicified in only a few thin sections (Table 1, Fig. 2). Silicified and unsilicified gastropods are present in nearly all of the thin sections but are proportionally rare. Gastropods appear granular under SEM, much like crinoids, and both internal molds and silicified skeletons occur in residue.

The thin sections reveal that silicification is patchy at both large and small scales. On the scale of an entire thin section, silicified regions are generally rare (point counts of silicified fossils are less than 5% of all points). On the scale of the individual fossil, incomplete silicification is typical in these assemblages, particularly in echinoderms and bivalves. Silicification of crinoid ossicles is generally limited to the outer surfaces, with the interior of the columnals typically remaining calcitic—a feature visible in both residue and thin section (Fig. 4A, B). In thin section, the silicified portion retains an outer coating of carbonate on some crinoid grains. Partial silicification of bivalves leads to extraction of small fragments in residue (see Fig. 4D–F). These observations demonstrate that silicified fossils, at least in the Virgin Limestone, are less abundant than calcitic ones, and the ways in which they are silicified plays a role in the bias we see in residue.

DISCUSSION

Petrographic Explanations for Residue Bias

The differences between thin section and residue numbers are substantial in many samples, implying that silicified assemblages, when taken alone, may send biased ecological signals (e.g., Butts and Briggs 2010). For example, the greater proportions of echinoderms in residue reflect preferential silicification relative to bivalves, as seen in thin section. Possible factors that may contribute to this preferential silicification include differences in shell mineralogy (aragonite vs. calcite), skeletal microstructure/texture (the porous surface of echinoderms, for example), typical shell size, or the presence of organic matter as a silica template (Froelich et al. 1979; Holdaway and Clayton 1982; Butts and Briggs 2010). Because thin sections and residues came from the same hand samples, environmental factors are minimized; the appearance of silicified crinoids millimeters from a non-silicified bivalve in thin section (see Fig. 4) suggest that in these assemblages, an originally aragonitic shell is not more likely to have been silicified than a calcitic skeleton.

Despite the biases in silicification, abundances measured by point counts do appear to show a positive correlation with abundances from acid residues for the major fossil groups preserved here, suggesting that meaningful paleoecological data can be gleaned from analyzing silicified faunas in the Virgin Limestone. For instance, if the purpose of a study is to examine the changes in abundant taxa through the stratigraphic section, this information should be retained in residue analysis. However, if a goal is to do a bed-by-bed identification of the ecologically dominant taxa, these data would at least occasionally reflect the selective silicification of crinoids and gastropods rather than their true abundances in the ancient community.

An important factor that must influence our results is the size distribution of silicified fossils: fossil fragments smaller than 0.5 mm, if identifiable, can be counted in thin section but are too small to examine in residue. This may be especially important for bivalve material, which was fragmented and often small in thin section and residue. Surprisingly, even with this size bias for bivalves, these organisms were the most likely to produce comparable abundances in thin section and residues (See Figs. 2, 3; samples SVMM12-46C and SVMM12-48B). Echinoderms typically show up in both residue and point counts of samples where they are present, but their relative abundances are notably different, and gastropods are fairly rare in thin section but are a common component of residues (e.g., SVU12-30, SVMM12-38).

Silicification was not fine-scale replacive but more granular and this, along with the different mineralogies of crinoids and gastropods, suggest a mechanism other than the selective fine-scale silicification of aragonite (Cherns and Wright 2000; Butts and Briggs 2010). Silicification of crinoid ossicles is generally limited to the outer surfaces, with the interior of the columnals typically remaining calcitic—a feature visible in both residue and thin section (see Fig. 4A, B). In thin section, the silicified portion retains an outer coating of carbonate on some crinoid grains. The preferential silicification of the outer surfaces of crinoids and both the shells and internal molds of gastropods may be related to the retention of organic matter after death for a longer interval in echinoderms and gastropods than in bivalves (e.g., Maliva and Siever 1988; Butts and Briggs 2010). The silicified rim in crinoid ossicles surrounds the area where organic matter would have been within the skeletal element (e.g., Macurda and Meyer 1975); gastropod shells could also retain a fair amount of organic matter in their shells for longer periods post-mortem or there may be more organic matter within the shell itself. In the bivalves, the most commonly silicified examples in these samples were identified as *Placunopsis* (identification was easier in thin section than in residue because bivalves were quite fragmented). *Placunopsis* bivalves in the Virgin Limestone commonly exhibit a “stacking” cemented life habit (Pruss et al. 2007) where organic matter might be retained for longer periods postmortem. Further, *Placunopsis* valves contain both aragonitic and calcitic portions of their shell microstructure, which may also affect their ability to silicify. Various pathways to silicification have been suggested (e.g., Butts and Briggs 2010), and these may play an important, yet unexplored, role in the types of biases present in silicified assemblages. For example, fine-scale silicification may produce greater fidelity with the actual fossil community, but this remains to be tested.

Comparisons to Other Silicified Faunas

The preferential silicification of certain taxa in the Virgin Limestone assemblages is similar to the hierarchy of silicification reported for some other faunas, and at least in our examples, it appears that the presence of organic matter is an important governing factor (e.g., Maliva and Siever 1988; Butts and Briggs 2010). Schubert et al. (1997) examined silicified faunas through time and found brachiopods and bivalves were the most commonly silicified fossils. Echinoderms also have a tendency to silicify, but gastropods were not noted. In the Virgin assemblage, echinoderms and gastropods are over-represented relative to their abundances in thin section, but it is this critical petrographic data that allow us to scrutinize the silicified assemblages. In only a handful of other assemblages have unsilicified and silicified faunas been compared directly (e.g., Cherns and Wright 2000)

←

FIG. 1.—Stratigraphic columns, showing measured sections at both localities of the Virgin Limestone Member, Moenkopi Formation in the Muddy Mountains of southern Nevada, USA (36°36'01 N 114°32'57 W, Muddy Mountains Overton locality; 36°32'51 N 114°36'50 W, Muddy Mountains Ute locality). All samples are indicated; samples that yielded silicified fossils are italicized (modified from Pruss et al. 2005).

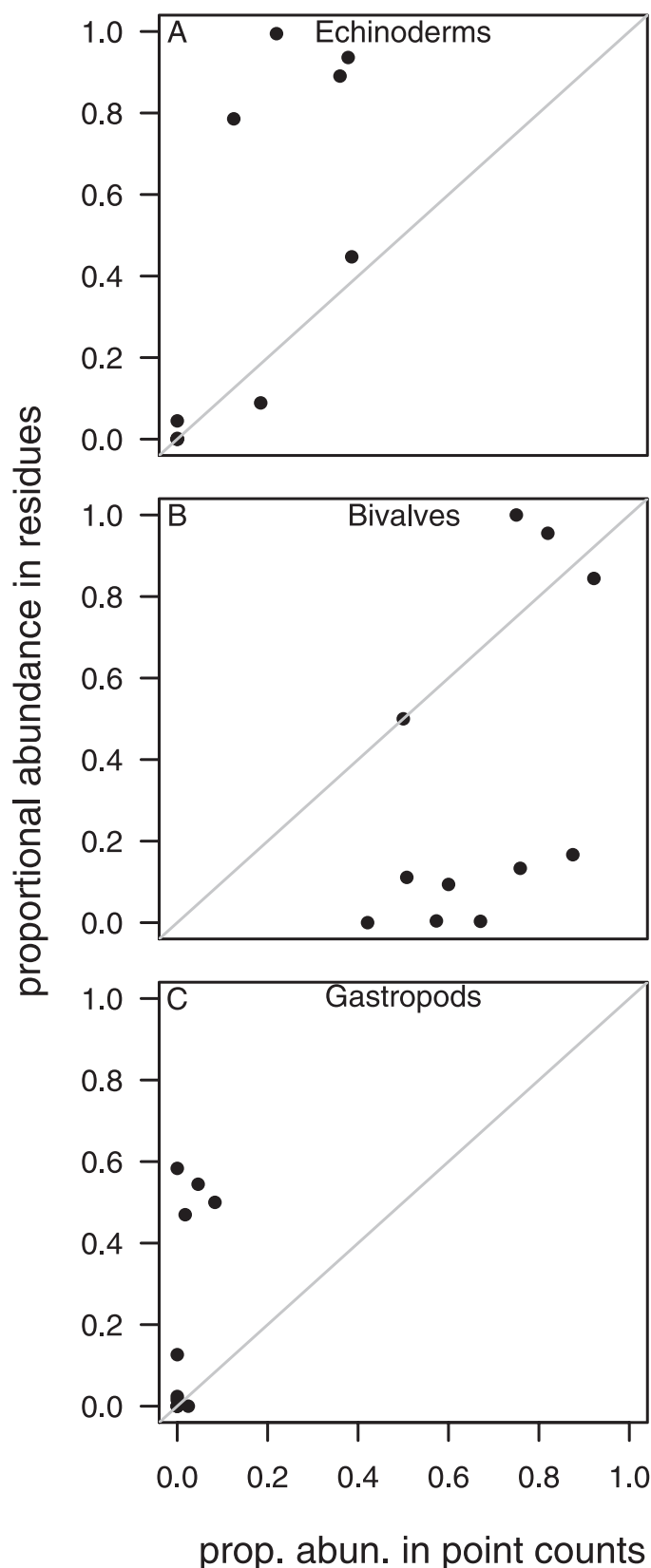


FIG. 2.—Scatterplots illustrating correlation between abundance measured by point counts versus abundance measured by counts of silicified specimens in acid residues. A) Echinoderms. B) Bivalves. C) Gastropods.

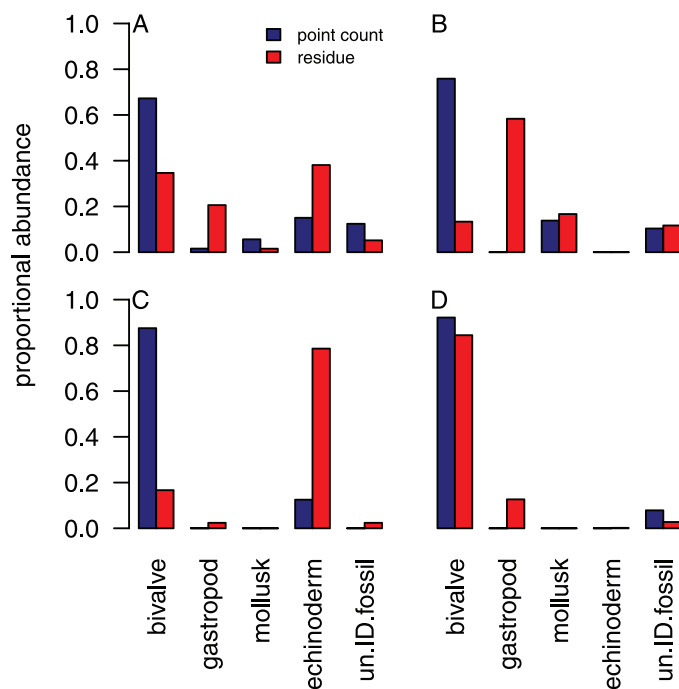


FIG. 3.—Pair bar graphs illustrating proportional abundance measured by point counts versus proportional abundance measured by specimen counts from acid residues showing all data and representative samples. A) Mean across all samples. B) Sample SVU 12-30. C) Sample SVU 12-33. D) Sample SVMM 12-46A.

At the assemblage scale, several differences emerge between faunas. In the Virgin Limestone assemblage, where silicification does not appear to have occurred after dissolution, aragonitic taxa are not selectively excluded from silicification as they are in the Permian Park City Formation (Schmitt and Boyd 1981), among others (Holdaway and Clayton 1982; Cherns and Wright 2000; Wright et al. 2003). Silicified, formerly aragonitic, gastropods are prevalent in Virgin residues, although small in size as in other silicified assemblages (Erwin and Kidder 2000), whereas bivalves make up a proportionally small part of the residue material relative to their abundance in thin section. In the case of the Silurian Gotland of Sweden, where there is thought to be excellent fidelity between silicified faunas and the original community, brachiopods and bivalves are some of the most commonly silicified taxa (Laufield and Jeppsson 1976). Importantly, these fossils were interbedded with bentonites, a common feature of silicified faunas throughout geologic time, but bentonites are not abundant in the Virgin Limestone Member. The degree to which bentonite-induced silicification provides greater fidelity of ecological interpretations is unknown but can be addressed in similar paired analyses.

The role of organic matter within an organism's shell has often been cited as a possible predictor of silicification but this has not been investigated in detail (Butts 2014; Butts and Briggs 2010). As an example, laboratory-produced petrified wood reveals the importance of organic matter providing a site for silica nucleation and the rapidity of silicification in systems where silica is not limiting (Alkhanee et al. 2004). Furthermore, organic matter in shells is found to survive several years postmortem, suggesting that the silicification process may not immediately follow death and yet may still be governed by the redox conditions fostered by organic matter decay (e.g., Butts 2014). In the case of the Virgin assemblages, the organic matter within the shell microstructure must be important in fostering the replacement of echinoderm ossicles, which can be seen in thin section (see Fig. 4). The

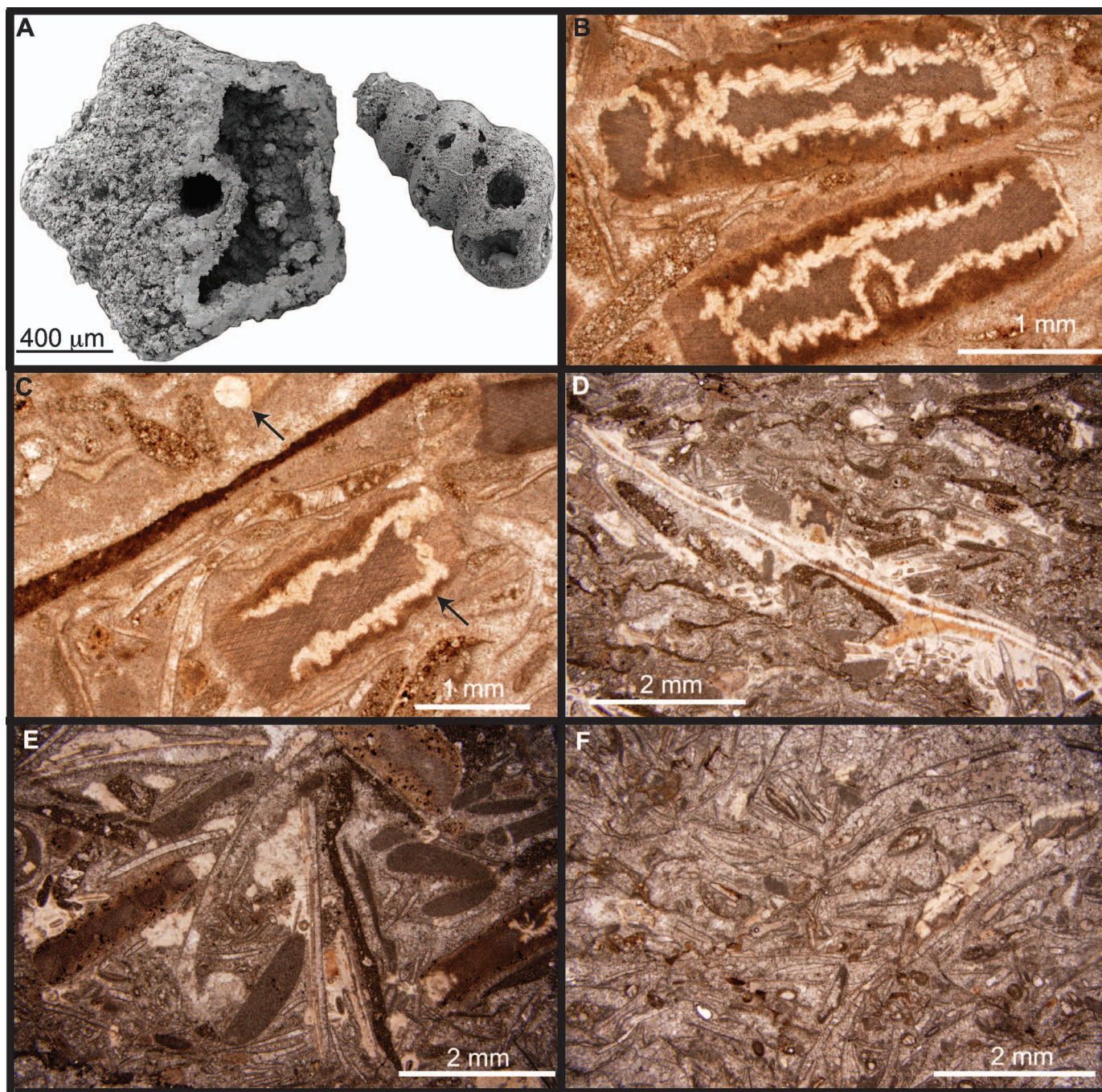


FIG. 4.—SEM images and photomicrographs of silicified fossils. A) Crinoid ossicle showing partial silicification of exterior and hollow interior; and silicified gastropod. B) Partially silicified crinoid ossicles showing micritized interior and exterior. C) Arrows show partially silicified crinoid ossicle and cross-section of an internal mold of a gastropod. D) Silicified bivalve shell with abundant non-silicified material. E, F) Bivalve-dominated thin sections showing patchy silicification and partial silicification of some valves.

abundance of gastropods in the Virgin assemblages may be governed by a similar process though this is less clear. It is possible that the organic matter within the shell was important or perhaps the organic matter from the decaying organism itself affected local redox conditions. The bivalves in this assemblage are predominantly thin and perhaps lacked sufficient organic matter in their shell to nucleate silica. The most commonly silicified bivalves in this Virgin assemblage have been identified as *Placunopsis* bivalves (Pruss et al. 2007), which perhaps contain more organic matter than other bivalves.

Sources of Silica

Silicified assemblages in the Virgin Limestone Member often occur at the horizon between interbedded carbonates and fluvial-marine siliciclastics. This observation suggests that local terrigenous siliciclastics might be the source of silica for the silicified faunas in the Muddy Mountains, similar to silicification in the Devonian Oriskany Sandstone of New York (Maliva 1992). While it is possible that the remobilization of silica from biogenic spicules and frustules also fostered silicification, no sponge

spicules or other siliceous organisms occurred in either residue or thin section in this study despite reports of siliceous sponges in some nearby sites (e.g., Brayard et al. 2011). It is possible that siliceous organisms were dissolved entirely post-mortem but this cannot be confirmed. The source and abundance of silica in silicified faunas may be yet another important factor that governs the nature of silicification and that may in part explain the variability between occurrence of fossilized organisms in silicified assemblages (e.g., Kidder and Erwin 2001; Butts and Briggs 2010). Particularly in the Early Triassic, it may be that silicified faunas are, in general, patchier and governed by local processes.

CONCLUSIONS

Silicified faunas are important repositories of information in the fossil record: they often preserve three-dimensional morphology of fossils and fine-scale characteristics of the original organism, and these assemblages have been used to reconstruct the diversity, ecology, and chemistry of critical intervals of Earth history (e.g., Clapham and Bottjer 2007; Beauchamp and Baud 2001). What remains less well understood is the nature of the biases that are introduced through the process of silicification. As we have shown in the Virgin Limestone Member of the Moenkopi Formation, variation in relative abundance of a given taxon is at least broadly preserved across samples but the relative abundances across taxa in silicified material from a given sample does not always closely approximate the organisms that are most abundant in the bulk rock as determined by petrographic examination. Pairing petrographic and residue analyses from additional sites and time intervals will be critical for further constraining the direction and magnitude of biases associated with diagenetic silicification of fossil assemblages, and for appropriately interpreting the diversity and ecology of paleocommunities, particularly from important intervals like recoveries from mass extinction.

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