

PALAIOS, 2021, v. 36, 95–114 Research Article DOI: http://dx.doi.org/10.2110/palo.2020.050



LITHOLOGICAL AND PALEOCOMMUNITY VARIATION ON A MISSISSIPPIAN (TOURNAISIAN) CARBONATE RAMP, MONTANA, USA

GARETT M. BROWN University of Georgia, Department of Geology, Athens, Georgia 30602-2501, USA email: gmb41807@uga.edu

ABSTRACT: The ecological structure of ancient marine communities is impacted by the environmental gradients controlling assemblage compositions and the heterogeneous distribution of sediment types. Closely spaced, replicate sampling of fauna has been suggested to mitigate the effects of such heterogeneity and improve gradient analyses, but this technique has rarely been combined with similar sampling of lithologic data. This study analyses lithological and faunal data to determine the environmental gradients controlling the composition of Mississippian fossil assemblages of the lower Madison Group in Montana. Eighty-one lithological and faunal samples were collected from four stratigraphic columns in Montana, which represent the deep-subtidal, foreshoal, and ooid-shoal depositional environments within one third-order depositional sequence. Cluster analysis identifies three distinct lithological associations across all depositional environments-crinoid-dominated carbonates, peloidal-crinoidal carbonates, and micritic-crinoidal carbonates. Cluster analysis and nonmetric multidimensional scaling (NMS) identifies a highly diverse brachiopod biofacies and a solitary coral-dominated biofacies along an onshore-offshore gradient. Carbonate point count data and orientation of solitary corals indicate that substrate and wave energy are two potential variables that covary with the onshore-offshore gradient. Overlaying lithological information on the NMS indicates a secondary gradient reflecting oxygen that is expressed by increasing bioturbation and gradation from brown to dark gray carbonates to medium-light gray carbonates. Taken together, these findings demonstrates how combining closely spaced, replicate sampling of lithologic and faunal data enhances multivariate analyses by uncovering underlying environmental gradients that control the variation in fossil assemblages.

INTRODUCTION

For ancient benthic marine communities, assemblage compositions are commonly associated primarily with an onshore-offshore gradient, also known as a water-depth gradient (Patzkowsky and Holland 2012). Water depth is a complex gradient that comprises other direct or resource environmental gradients (Whittaker 1956; Austin et al. 1984), such as temperature, substrate, sunlight penetration, oxygenation, nutrients, shear stress, and salinity (Tait and Dipper 1998). Species abundances change along these environmental gradients in keeping with their specific ecological niches, giving rise to community changes along onshoreoffshore or water-depth gradients. Examination of the lithological data (i.e., grain size, grain composition, bioturbation levels, and biogenic structures) as well as the ecological characteristics of assemblages (i.e., life mode and feeding ecology) indicate that substrate and wave-energy gradients can commonly be identified in the fossil record (Cisne and Rabe 1978; Lafferty et al. 1994; Patzkowsky 1995; Holland et al. 2001; Webber 2002; Novack-Gotshall and Miller 2003; Scarponi and Kowalewski 2004; McMullen et al. 2014; Scarponi et al. 2014; Zuschin et al. 2014). Evaluating these same lithological and faunal characteristics has also identified primary and secondary gradients that are uncorrelated with water depth such as substrate (Holland et al. 2001; Tomašových 2006; Redman et al. 2007; Perera and Stigall 2018), oxygenation (Olszewski and Patzkowsky 2001), wave energy (Scarponi and Kowalewski 2004; Bush and Brame 2010), and salinity (Scarponi and Kowalewski 2004).

Interpreting ancient environmental gradients is also impacted by the spatial distribution of fossils along bedding surfaces and within depositional environments (Bennington 2003; Webber 2005; Perera and

ssils along bedding surfaces and within gradients. The lower Madison Bennington 2003; Webber 2005; Perera and crinoids (Laudon and Severs

Stigall 2018). Fossil distributions are usually heterogeneous, such that a count for a single bed may not sufficiently characterize the communities within the depositional environment (Kidwell and Bosence 1991; Bennington 2003; Webber 2005). Additionally, the lithological record is heterogeneous at small spatial scales, especially within carbonate systems, where varying percentages of sediment grains, matrix, and bioturbation intensity indicate multiple microfacies within a depositional environment (Flügel 2010). If only a few samples are collected from either an outcrop or locality, the patterns in faunal or lithological variation may simply reflect the patchiness of the community or environment, and any ecological analyses may be unable to explain the full scope of biotic or abiotic gradients as a result (Bennington 2003; Webber 2005; Flügel 2010). This is exemplified by studies in the Ordovician Kope Formation of Ohio (Webber 2005) and the Cretaceous of New Jersey (Bennington 2003) where limited sampling identified the broad ecological patterns, but replicate sampling was required to discern the drivers of fine-scale differences of faunal distributions. To account for the heterogeneous nature of the fossil and lithological records when examining environmental gradients, closely spaced, replicate sampling of faunal and lithological samples is needed from the same depositional environment at each sampling locality (Bennington 2003; Webber 2005; Patzkowsky and Holland 2012; Perera and Stigall 2018).

The Mississippian lower Madison Group in Montana is an excellent location to examine the effect of heterogeneity in faunal distributions and lithological characteristics on the interpretations of environmental gradients. The lower Madison Group contains diverse assemblages of crinoids (Laudon and Severson 1953), brachiopods (Shaw 1962;



FIG. 1.—Study sites and paleogeography of the lower Madison Group. Study sites are noted by black circles and cities by white circles. Light blue indicates shallow carbonate shelves and darker blues indicate deeper-water carbonate basins. Modified from Smith et al. (2004).

Rodriguez and Gutschick 1968, 1969; Christensen 1999), rugose corals (Sando 1960; Waters and Sando 1987) and other benthic invertebrates across multiple depositional environments (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). Here I build upon previous investigations of the lower Madison Group (i.e., Elrick and Read 1991; Sonnenfeld 1996, Smith et al. 2004) to provide detailed descriptions of the lithofacies, sequence stratigraphy, and faunal distributions within lessstudied regions of the Madison Shelf. This framework is used to test the efficacy of high-resolution, replicate sampling of lithological data and faunal counts in answering two main questions. First, can replicate sampling distinguish environmental gradients that covary with and therefore create the water-depth gradient? Second, can additional gradients unrelated to water depth be identified? In answering these questions, this study shows how the collection of replicate lithological data in conjunction with faunal data will allow lithological information to be directly linked to each assemblage, potentially expanding the number of environmental gradients that can be identified in the fossil record.

GEOLOGIC SETTING

The study area encompasses the fossiliferous members of the lower Madison Group in the Central Montana Trough and northwestern Montana (Fig. 1). Conodont biostratigraphy places the lower Madison Group within the lower to middle Tournaisian (approximately 357–353 Ma; Gutschick et al. 1980; Sando 1985; Cohen et al. 2013) (Fig. 2). The lower Madison Group is exposed in Wyoming, Idaho, Montana, and North Dakota in the United States (Andrichuk 1955; Mudge et al. 1962; Moore 1973; Sando 1976; Poole and Sandberg 1977; Gutschick et al. 1980) and Alberta and Saskatchewan in Canada (Johnston et al. 2010).

The Mississippian Madison Group is part of a carbonate ramp system that extended from New Mexico to western Canada (Gutschick et al. 1980; Maughan 1983; Smith et al. 2004). In the Mississippian, this area was bounded by the Transcontinental Arch to the east and the Antler Highlands to the west (Fig. 1; Gutschick et al. 1980; Gutschick and Sandberg 1983; Maughan 1983; Smith et al. 2004), and it was located approximately 0–10° north of the equator (McKerrow and Scotese 1990). Although it has been studied mostly along the shallow portions of the ramp, the Madison Group also includes deeper-water facies of the Antler Foreland Basin, the Williston Basin, and Central Montana Trough (Fig. 1; Gutschick et al. 1980; Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004).

In Montana, Idaho, and western Wyoming, the lower Madison Group unconformably overlies Devonian carbonate and siliciclastic rocks of the



FIG. 2.—Chronostratigraphic and lithostratigraphic framework of the Madison Group carbonates and underlying Upper Devonian Sappington Formation in southwestern, central, and northwestern Montana. Modified from Elrick and Read (1991), Sonnenfeld (1996), and Johnston et al. (2010). Correlations based on Gutschick et al. (1980) and Sando (1985). Time scale is from Cohen et al. (2013).

Beirdneau, Darby, and Three Forks formations (Gutschick et al. 1980), but in central Wyoming, the Madison Group overlies the Ordovician Bighorn Dolomite (Gutschick et al. 1980). In the study area, the lower Madison Group is represented by the Lodgepole Formation in central and southwestern Montana and by the Allan Mountain Limestone in northwestern Montana. These formations unconformably overlie the Upper Devonian Sappington Formation, a yellow-tan siliciclastic member of the Three Forks Group (Fig. 2; Mudge et al. 1962; Gutschick et al. 1980). The lower Madison Group is overlain by members of the upper Madison Group. In central and southwestern Montana, the Lodgepole Formation is conformably overlain by the Mission Canyon Formation, and in northwestern Montana the Allan Mountain Limestone is overlain by the Castle Reef Dolomite (Fig. 2). In central and southern Montana and Wyoming, the upper Madison Group is unconformably overlain by the Pennsylvanian Amsden Formation (Gutschick et al. 1980; Sonnenfeld 1996), whereas in northwestern Montana and southern Alberta, the Madison Group is unconformably overlain by the Middle Jurassic Sawtooth Formation (Cobban 1945; Gutschick et al. 1980).

The Lodgepole Formation and Allan Mountain Limestone represent wave-dominated attached carbonate ramp system that include peritidal, shoal, foreshoal, deep subtidal, and offshore environments characterized by storm beds in distal facies (Fig. 3; Elrick and Read 1991; Chen and Webster 1994; Sonnenfeld 1996; Smith et al. 2004). The Mission Canyon Formation and the Castle Reef Dolomite of the overlying upper Madison





FIG. 3.—Onshore-offshore distribution of carbonate facies on the Madison shelf. Based on Elrick and Read (1991).

Group are dolomitized, crinoidal grainstones deposited in inner ramp and peritidal carbonate environments (Mudge et al. 1962; Reid and Dorobek 1993).

Previous sequence-stratigraphic interpretations of the lower Madison Group have focused primarily on the Lodgepole Formation in Wyoming and southwestern Montana (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). Two (Sonnenfeld 1996) to three (Elrick and Read 1991) third-order sequences are recognized in the Lodgepole Formation within the Madison Shelf of Wyoming and southern Montana (Elrick and Read 1991; Sonnenfeld 1996). Down depositional dip into the Central Montana Trough, the distinction between these sequences becomes less clear and sequence boundaries pass into correlative conformities (Elrick and Read 1991). The sequence-stratigraphic frameworks established along the Madison Shelf (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004) are applied to contextualize lithofacies and biofacies changes within the lower Madison Group in the Central Montana Trough and northwestern Montana.

METHODS

Data Collection

Four stratigraphic columns of the lower Madison Group (the Lodgepole Formation and Allan Mountain Limestone) were measured in central and western Montana during the summer of 2018 and 2019 (Fig. 1). Localities were chosen based on site accessibility and to maximize paleogeographic coverage. Each column was measured with a Jacob staff demarcated in 0.1 m intervals and a Brunton transit. At each column, beds were described according to lithology, carbonate grain type (i.e., skeletal, ooid, peloid, etc.), bed thickness, bioturbation index, sedimentary structures, trace-fossil diversity, and fossil fragmentation. Carbonate lithology was classified following Dunham (1962), bed thickness following Ingram (1954), and intensity of bioturbation (ichnofabric index–ii) following Droser and Bottjer (1986). Lithological descriptions were used to classify beds and bedsets by lithofacies along the carbonate ramp using the facies model of Elrick and Read (1991).

Eighty-one field counts of fossils were conducted among the four columns. For each field count, lithology, stratigraphic position, and taphonomic features of fossils were recorded. Most (52) field counts were conducted along bedding surfaces wherever possible to reduce the amount of time-averaging. *In situ* bedding surfaces were preferentially targeted as to preserve the stratigraphic context of the field count. Multiple field counts were conducted along some bedding surfaces to examine the lateral heterogeneity of assemblages; such replicate counts were a minimum 15 m apart. Some (25) field counts were conducted along vertical rock faces, where fossiliferous horizons could be constrained to less than 10 cm vertically. A few (5) field counts from the Crystal Lake road cut were conducted on float samples that could be constrained to a specific interval within the stratigraphic column using lithological characteristics such as bed thickness, carbonate lithology, and bioturbation intensity.

For each field count, fossils were counted for thirty minutes or until at least two species and twenty-four individuals were reached, whichever took the greater amount of time. Fossil specimens were identified to species where possible, although preservation of some brachiopods and solitary corals required identification at the genus or family level. Most bryozoans and crinoids were identified to order or morphological form (i.e., trepostome or fenestrate, round or elliptical crinoid ossicle), except where calices were well preserved. I performed all field counts and species identifications to ensure taxonomic and sampling consistency.

The minimum number of individuals (MNI) was calculated in several ways based on taxonomic group (see Patzkowsky and Holland 2012). For brachiopods and bivalves, the MNI was calculated as the sum of the number of articulated specimens, the greater amount of brachial or pedicle and left or right valves respectively, and one-half of the number of indeterminate valves. Colonial corals were counted as individuals based on the cohesiveness of corallites. Clusters of corallites that greater are than 10 centimeters apart from another were counted as separate individuals. Every 3-cm length of bryozoan was treated as an individual to provide a rough standardization by biovolume (see Holland and Patzkowsky 2004). For trilobites, the MNI was counted as the maximum number of either cranidia or pygidia, whichever is greater. For gastropods and solitary corals, the MNI is the number of complete apices or calices. The MNI of crinoids was not calculated because individuals disarticulate into ossicles that became the dominant skeletal grain of most field counts. For crinoids, presenceabsence data was used instead for the various morphospecies of crinoid ossicles, except where calices could be identified.

Eighty-one lithological samples were collected from the same beds as the faunal counts to confirm field identification of lithology and to quantify lithological properties of the faunal counts. Thin sections were prepared from these samples and counted to 300 points. Point counts were conducted using a two-dimensional grid, and every component that intersected grid point was counted (sensu Flügel 2010). These counts include the components of grain type, micrite, cement, quartz, authigenic minerals and pore space. The hue, value, and chroma of each hand sample was estimated on a freshly cut surface using the Munsell Color System (Munsell Color 1976). While the use of color is not common in lithologic analyses of carbonates, differences in lithologic color can be used to assess potential variations in oxygenation, organic content, and redox state (see Flügel 2010, p. 53-54 and references therein for review). Additional lithological samples from non-fossiliferous beds were collected to confirm field identification of lithology but were not used in subsequent data analyses. Photographs of the thin sections are available at the Figshare online repository (https://doi.org/10.6084/m9.figshare.13350869).

Data Analysis

Before statistical analysis, the point-count and the species-abundance matrices were culled to remove rare petrographic components and species. Components with proportional abundances less than 5% of the overall petrographic assemblage were removed from the point-count matrix. Species with proportional abundances and less than 1% of the overall species assemblage were removed from the species-abundance matrix. This reduced the petrographic components from 23 to 14, and the number of species from 84 to 20 species. This culling removes the rare carbonate components and fossil species, which improves figure clarity and their interpretations by reducing the number of data points without removing the diagnostically important petrographic components and species.

Data standardizations were applied to the culled components and species-abundance matrices. The culled components matrix underwent the percent maximum standardization as sample sizes were already standardized to 300 counts, and analyses needed to account only for variations in component abundances. The culled species-abundance matrix received percent sample standardization followed by percent maximum standardization of each species to account for variations in both sample size and species abundance. All statistical analyses were performed on these culled matrices using R Version 3.6.2 (R Core Team 2019). The faunal dataset, the point count dataset, the taxonomic and lithological properties, and the R script are archived with the Online Supplemental File.

Q-mode cluster analysis was performed separately on the culled components and species-abundance matrices to identify the compositional and taxonomic similarities between samples. Q-mode clusters were identified using the *cluster* package (Maechler et al. 2019). Q-mode cluster analysis used Bray-Curtis dissimilarity for the distance matrices and Ward's Method for linkage method. Ward's Method minimizes the increase of error in the sum of squares distances between samples, and it produces compact, well-defined clusters (McCune and Grace 2002).

The R-mode cluster was performed separately on the culled components and species-abundance matrices to identify co-occurring components and species. R-mode clusters were also identified using the *cluster* package (Maechler et al. 2019). R-mode cluster analysis also used Bray-Curtis dissimilarity for the distance matrices and Ward's Method for linkage method.

Two-way cluster analysis was performed separately on the culled components and species-abundance matrices to define petrographic clusters and biofacies. Two-way clusters were calculated by using the *pheatmap* package (Kolde 2019). This package combines the Q-mode and R-mode analyses, and it displays the proportional abundances of the components or species within each sample, which assists in identifying the different petrographic clusters and biofacies.

Nonmetric Multidimensional Scaling (NMS) of the culled speciesabundance matrix was performed to identify environmental gradients correlated with assemblage variations. NMS was performed using the metaMDS function in vegan package (Oksanen et al. 2019). It used a percent sample standardization on the culled species-abundance matrix, Bray-Curtis dissimilarity matrix, three dimensions, and 50 restarts to avoid local optima. The number of dimensions used in NMS is typically selected based on stress values, which represents the goodness of fit between the original distance matrix and the reduced distance matrix of the ordination (McCune and Grace 2002). The NMS in three dimensions calculated stress to be 0.146, which is within the acceptable range for interpreting NMS results (less than 0.2 is preferred for ecological studies; Kruskal 1964a; Clarke 1993; see McCune and Grace 2002 for review), and additional dimensions provided subsequently smaller reductions in stress values. The metaMDS function rotates the NMS solution using a principal components analysis (PCA) such that NMS axis 1 reflects the most source of variation and higher axes reflect progressively less variation. Environmental variables were overlain on the NMS ordination using the envfit function in the vegan package (Oksanen et al. 2019). Variables used in envfit include component percentages, bioturbation index, hue, and color value. The envfit function correlates variables in a secondary matrix with sample scores from the NMS, allowing environmental variables to be displayed as vectors within the ordination space. The direction and length of a vector identifies how well that variable is correlated to each NMS axis.

RESULTS

Carbonate Facies Association Descriptions

The lower Madison Group carbonate ramp preserves carbonate facies associations from six depositional environments—the offshore, deep subtidal, the foreshoal, ooid shoal, crinoid shoal, and peritidal (Fig. 3, Table 1). These facies associations were interpreted using only lithological data, and they do not consider faunal associations as to avoid circularity when interpreting environmental gradients. **Offshore.**—Thinly-bedded, planar laminated, unfossiliferous dark gray carbonate mudstone interbedded with very thin shale beds (Fig. 4A–4C) indicate a dysoxic offshore environment with a poorly developed infauna (Elrick and Read 1991; Sonnenfeld 1996; Boyer and Droser 2011). The presence of planar lamination within these carbonate mudstones and lack of wave or current structures suggests deposition below storm-wave base (Elrick and Read 1991; Burchette and Wright 1992; Sonnenfeld 1996). The alternations between carbonate and siliciclastic lithologies reflects either variation in storm intensity along the ramp (Elrick et al. 1991) or sediment input via gravity flows and suspension (Sonnenfeld 1996). The ratio of carbonate mudstone to shale increases up-section, indicating an increase in shear stress that is consistent with a transition from the distal offshore (Fig. 4A) to the proximal offshore environments (Fig. 4B).

Deep Subtidal.—Thin-bedded, moderately bioturbated (ii2-ii4, sensu Droser and Bottjer 1986), dark gray skeletal packstone interbedded with yellow-tan shale to argillaceous partings (Fig. 4D) with diverse fossil assemblages suggest deposition in the subtidal. Ichnofossils identified include Taenidium?, Zoophycos (Fig. 4E, 4F), and other horizontal feeding and burrowing traces as well as Thalassinoides and other vertical burrows. Fossils include crinoid ossicles and calices, fenestrate and trepostome bryozoans, brachiopods, and solitary corals (Fig. 4G). The increase in ichnofabric index, presence of burrows, and diversity of skeletal material in this facies association suggests more oxic conditions than in the offshore facies association (Droser and Bottjer 1986; Boyer and Droser 2011), although the variation in ichnofabric index and planar lamination may indicate variable oxygen levels (Boyer and Droser 2011). Bedforms and sedimentary structures such as vortex ripples, wave-ripple lamination (Fig. 4H) and planar lamination are present but rare. Vortex ripples and waveripple lamination indicates reworking by storm waves (Elrick and Read 1991; Burchette and Wright 1992; Sonnenfeld 1996) and the argillaceous drapes represent settlement of terrigenous material during fair-weather conditions (Elrick and Read 1991). Dense fossil concentrations along thin argillaceous bedding surfaces indicate sedimentation rates from settlement were slow within the deep-subtidal (Elrick and Read 1991; Kidwell and Bosence 1991).

Foreshoal.-Two lithofacies are identified in this association representing two depositional environments. The most common lithofacies is the medium-bedded, bioturbated (ii3-ii5; sensu Droser and Bottjer 1986), fossiliferous, medium gray skeletal-peloidal grainstone (Fig. 5A, 5D) with planar lamination and silicified vertical and horizontal burrows. The presence of burrows and greater ichnofabric indices indicate oxic conditions similar to the deep subtidal facies (Boyer and Droser 2011). However, variation in ichnofabric index may result from fluctuations in oxygen levels (Droser and Bottjer 1986; Boyer and Droser 2011) or from variations in sedimentation rate (see Shourd and Levin 1976; Taylor et al. 2003), which are estimated to range from 0.3 to 1.0 m/kyr (Elrick and Read 1991). Fossils include crinoid ossicles, solitary corals (Fig. 5F), colonial corals, brachiopods, and mollusks. The increase in abundance of coarse skeletal grains indicates that this lithofacies was deposited within fairweather wave base (Elrick and Read 1991; Burchette and Wright 1992; Sonnenfeld 1996). Sedimentary structures typical of the foreshoal on carbonate ramps such as hummocky, tabular, or trough cross-stratification (Elrick and Read 1991, Sonnenfeld 1996) were not observed, possibly as the result of bioturbation obscuring such sedimentary features. The skeletal grainstone lithofacies likely represents a skeletal shoal or bank subenvironment within the foreshoal facies association that was deposited in somewhat deeper water than the ooid-shoal facies association (Elrick and Read 1991; Smith and Read 2001).

The second lithofacies within the foreshoal facies association is a medium-bedded, bioturbated (ii3-ii5; *sensu* Droser and Bottjer 1986), fossiliferous dark-gray carbonate mudstone (Fig. 5B, 5E). Silicified

TABLE	1.—0	Carbonate	facies	associations	of	`the	lower	Madison	Group.
			/		./				

Facies	Lithology	Sedimentary and biogenic	Fossila	Competers and contract relationships
associations	Littiology	structures	FOSSIIS	Geometry and contact relationships
Offshore	Very thin- to thin-bedded dark gray carbonate mudstone. Commonly interbedded with dark gray to black shales. Commonly expresses as vegetated covered interval.	Planar lamination abundant. Ichnofabric index ii1	None observed	Tabular. Sharp basal contact. Grades upwards into deep-subtidal facies association.
Deep subtidal	Thin bedded, medium to dark gray skeletal packstone with tan argillaceous partings	Vortex ripples, wave-ripple lamination, and planar lamination rare. Ichnofabric index ii2–ii4; <i>Zoophycus, Thalassinoides</i> and <i>Taenidium</i> ?	Whole fossils and coarse fragments of crinoids, fenestrate and trepostome bryozoans, brachiopods, solitary corals and proetid trilobites	Tabular. Gradationally overlies offshore association and is gradationally overlain by the foreshoal association.
Foreshoal	Medium-bedded medium to light gray skeletal, peloidal, oolitic grainstone	Planar lamination rare Ichnofabric index ii3–ii5; silicified vertical and horizontal burrows	Whole fossils and coarse fragments of crinoids, solitary corals, colonial corals, brachiopods, and mollusks	Tabular. Gradationally interbedded with carbonate mudstone lithofacies. Gradationally overlies deep-subtidal association and gradationally overlain by ooid-shoal association
Foreshoal	Medium-bedded dark gray carbonate mudstone	Planar lamination rare; Ichnofabric index ii3–ii5; Silicified <i>Thalassinoides</i> and other burrows	Whole fossils and coarse fragments of crinoids, solitary corals, colonial corals, brachiopods	Tabular. Gradationally interbedded with skeletal-oolitic grainstone lithofacies
Ooid shoal	Medium-bedded, medium to light gray oolitic grainstone	Small-scale cross-stratification common Ichnofabric index ii1–ii4	Whole and coarse fossil fragments of crinoids, solitary corals, brachiopods occasionally observed.	Tabular. Gradationally overlies skeletal-ooid grainstone of the foreshoal association. Gradationally overlain by crinoid-shoal and peritidal associations
Crinoid shoal	Thin to medium-bedded tan crinoidal grainstone	None observed Ichnofabric index ii4	Only coarse crinoid ossicles	Tabular. Gradationally overlies ooid- shoal association. Gradationally overlain by peritidal association
Peritidal	Thin to medium-bedded light gray carbonate mudstone where exposed. Commonly expresses as vegetated covered intervals up section of the foreshoal and ooid-shoal facies.	Well-laminated; Brecciation and silicified grikes common Ichnofabric index ii1	None observed.	Tabular. Gradationally overlies ooid- shoal and crinoid-shoal associations. Upper contact is sharp.

vertical and horizontal burrows such as *Thalassinoides* are common (Fig. 5C). Fossils include crinoid ossicles and calices, solitary corals, colonial corals, and brachiopods. Ichnofabric indices, intense burrowing, and high fossil diversity indicate that this lithofacies was deposited in an oxygenated environment similar to the skeletal grainstone lithofacies (Droser and Bottjer 1986; Boyer and Droser 2011). Sedimentary structures are rare, with rare planar lamination, indicating less influence of waves. The carbonate mudstone lithofacies likely represents a muddy intershoal deposit in a topographic low protected from waves between the skeletal bank deposits within the foreshoal facies association (Elrick and Read 1991).

Ooid Shoal.—This facies association is characterized by mediumbedded, medium to light gray oolitic grainstone (Fig. 5G). Bioturbation levels vary, with ichnofabric index ranging from ii1–ii4. Small scale cross stratification can be observed in beds that have little bioturbation (Fig. 5H), indicating deposition in a high shear stress setting above fair-weather wave base. Color and ichnofabric index indicate that the ooid-shoal facies association was well-oxygenated (Berner 1981; Maynard 1982; Droser and Bottjer 1986; Boyer and Droser 2011). Fossils are rare, but include crinoid ossicles, solitary corals, and brachiopods.

Crinoid Shoal.—Overlying the ooid-shoal facies association is a thin to medium-bedded, tan crinoidal grainstone (Fig. 5G). No sedimentary or biogenic structures are observed, and coarse crinoid ossicles (i.e., greater than 2 mm) are the only fossils identified. Its position above the ooid-shoal facies association, and the low faunal diversity and abundance indicates that this association was deposited in a restricted lagoon (Sonnenfeld 1996). The tan color is caused by intense dolomitization (Flügel 2010). In near shore environments, dolomitization is commonly caused by evaporation, seepage reflux, seawater pumping, subsurface burial, or synsedimentary dolomitization that is mediated by bacterial sulphate reduction or methanogensis (Tucker and Wright 1990; Melim and Scholle 2002; Machel 2004; Flügel 2010; Meister et al. 2013). It is impossible to determine the exact dolomitization mechanism without geochemical data or the presence of evaporites (Tucker and Wright 1990; Flügel 2010).

Peritidal.—This facies association is characterized by non-fossiliferous, non-bioturbated (ii1; *sensu* Droser and Bottjer 1986), thin to mediumbedded, light gray carbonate mudstone (Fig. 5I). The lack of fossils and low bioturbation intensity indicates this facies was also deposited within restricted conditions, and its position above the crinoid-shoal facies association suggests this facies was deposited in the peritidal environment (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). Laminated beds are interbedded with non-laminated beds. Laminations are interpreted as algal in origin as they are slightly irregular and not completely planar (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004).



Fig. 4.—Offshore and deep-subtidal facies. A) Interbedded shale and thin-bedded carbonate mudstone of the distal offshore facies association, Sappington Canyon, 30 m. B) Thin-bedded carbonate mudstone of the proximal offshore facies association, Sappington Canyon, 30 m. C) Well-preserved planar lamination within the offshore carbonate mudstone of the offshore facies association, Sappington Canyon, 30 m. D) Thin-bedded skeletal packstone with argillaceous to shale partings of the deep-subtidal facies association, Milligan Canyon, 21 m. E) *Taenidium*? (T) and other horizontal burrows (h) on bedding surface within the deep-subtidal facies association, Crystal Lake, 108 m. F) *Zoophycos* (Z) ichnofossil along bedding surfaces in the deep-subtidal facies association, Milligan Canyon, 2 m. G) Shell hash within the deep-subtidal facies association with bryozoans, crinoid ossicles, and brachiopod fragments, Milligan Canyon, 2.5 m. H) Wave-ripple lamination in the deep-subtidal facies association, Crystal Lake, 58 m.

Sequence-Stratigraphic Architecture

One third order depositional sequence is identified in the lower Madison Group at all four localities (Fig. 6). The lower sequence boundary (SB1) is placed at the contact between the lower Madison Group and the underlying Sappington Formation (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). This contact is present at Sappington Canyon, but was not observed at the other localities. A talus-covered interval beneath the measured section at Gibson Reservoir covers the contact and obscures the relationship between the Allan Mountain Limestone and the underlying Sappington Formation. The Sappington Formation is not exposed at Milligan Canyon as a poorly lithified conglomerate covers the Lodgepole



FIG. 5.—Foreshoal through peritidal facies. A) Medium-bedded skeletal grainstone of the foreshoal facies association cap most parasequences, Milligan Canyon, 3 m. B) Medium-bedded carbonate mudstone interbedded with bedsets of the skeletal grainstone of the foreshoal facies association, Milligan Canyon, 46 m. C) Silicified burrow within the foreshoal facies association, Sappington Canyon, 93 m. D) Medium-bedded skeletal grainstone of the foreshoal facies association, Gibson Reservoir, 234 m. E) Medium-bedded carbonate mudstone interbedded with bedsets of the skeletal grainstone of the foreshoal facies association, Gibson Reservoir, 234 m. E) Medium-bedded carbonate mudstone interbedded with bedsets of the skeletal grainstone of the foreshoal facies association, Gibson Reservoir, 4 m. F) Solitary corals of the foreshoal facies association, Gibson Reservoir, 238 m. G) Medium bedded oolitic grainstone and tan, dolomitized crinoidal grainstone of the ooid-shoal and crinoid-shoal facies associations, Milligan Canyon, 64 m. H) Ooid grainstone with small scale cross-stratification, Milligan Canyon, 54 m. I) Peritidal facies association consist of planar laminated carbonate mudstone cut by silicified grikes, Sappington Canyon, 224 m.

Formation down section. While the Sappington Formation is not exposed along the road cut at Crystal Lake, it is present in less accessible places nearby.

The lowstand systems tract (LST) is observed only at Crystal Lake, where it is characterized by shallowing-upward offshore through foreshoal deposits to foreshoal deposits showing no net trend in water depth. Here, the LST is capped by a transgressive lag of iron-stained chert, mudstone pebble, and skeletal grains overlain by deepening-upward deep-subtidal deposits. At Sappington Canyon, the contact between the lower Madison Group and the underlying Sappington Formation is interpreted as both the



sequence boundary and the transgressive surface, as deepening-upward parasequences are identified immediately above this contact indicating the transgressive systems tract (TST). At Milligan Canyon, the measured section begins above a thrust fault, and the base of the Lodgepole Formation is not exposed. At Gibson Reservoir, talus obscures the base of the lower Allan Mountain Limestone, preventing assessment of stacking patterns to determine if the LST was present.

The transgressive surface is present at Sappington Canyon and Crystal Lake. At Sappington Canyon, it is combined with SB1, and the overlying parasequences are deepening upwards, indicating the TST. At Crystal Lake, the transgressive surface is identified as the lag of iron-stained carbonate rock, mudstone pebble, and skeletal grains.

The transgressive systems tract (TST) is present at all localities, and it is defined by the upsection loss of shallower facies associations and the presence of deepening-upward parasequences. At Milligan Canyon and Crystal Lake, the foreshoal facies association is lost upsection, the deepsubtidal facies association decreases in thickness, and the offshore facies association appears and increases in its percentage of shale. At Sappington Canyon, the foreshoal and deep-subtidal facies associations are lost upsection, and the TST is mostly represented by the offshore facies association, although it is largely covered by vegetation. At Gibson Reservoir, no facies are lost upsection, and the TST is represented by a thick package of carbonate mudstone of the foreshoal facies association at the base of the section. The thickness of the TST is similar at all localities, approximately 20 m at Sappington Canyon and Milligan Canyon, approximately 25 m at Gibson Reservoir, and approximately 30 m at Crystal Lake.

The maximum flooding zone (mfz) is present at all localities (Fig. 6). At Milligan Canyon and Crystal Lake Road, the maximum flooding zone is represented by a shale interval interbedded with thin-bedded skeletal packstone. At Sappington Canyon, the maximum flooding zone is represented by a covered interval with a few exposed very thin beds of carbonate mudstone interbedded with shale. At Gibson Reservoir, the maximum flooding zone is represented by a thick interval of mediumbedded carbonate mudstone overlain by a single bed of skeletal grainstone near the base of the measured section (Fig. 6).

The highstand systems tract (HST) is present at all localities, and it is recognized by aggradationally stacked to shallowing-upward parasequences. At Gibson Reservoir, the HST is approximately 280 m thick and parasequences shallow upwards from carbonate mudstone lithofacies to the skeletal grainstone lithofacies of the foreshoal facies association. Parasequences shallow upwards into the peritidal facies association at 315 m in the section. At Sappington Canyon, the HST is approximately 225 m thick and begins as the offshore facies association with parasequences showing no net trend in water depth. Parasequences then shallow upwards from offshore to deep-subtidal, then offshore to foreshoal, carbonate mudstone lithofacies to skeletal grainstone lithofacies within the foreshoal, foreshoal to ooid-shoal, and finally ooid-shoal into peritidal facies. At Milligan Canyon, the HST is approximately 50 m thick and includes one parasequence that shallows upward from offshore to foreshoal facies associations and a second one that shallows upward from offshore to crinoid-shoal facies associations. Four to five additional parasequences that shallow upward from ooid shoal through peritidal are present at the top of the Milligan Canyon column but placing them into stratigraphic context was impossible, owing to changing bed geometries and dense vegetation. At Crystal Lake, the HST is approximately 85 m thick and includes parasequences of deep-subtidal facies association that show no net trend in water depth for approximately 30 m, followed by shallowing-upward parasequences of deep-subtidal facies to foreshoal capped by ooid-shoal facies associations.

The upper sequence boundary (SB2) is present only at Gibson Reservoir and Sappington Canyon, where it is placed at as the contact between the peritidal facies association of the lower Madison Group and the poorly bedded, crystalline grainstone of the upper Madison Group. At Gibson Reservoir, SB2 separates the well-bedded foreshoal and peritidal of the Allan Mountain Limestone from the poorly bedded, recrystallized grainstone of the Castle Reef Dolomite. At Sappington Canyon, SB2 separates the peritidal facies association of the Lodgepole Formation with well-bedded carbonate mudstone and silicified grikes from the poorly bedded, recrystallized grainstone of the Mission Canyon Formation. These silicified grikes are vertical karst fissures (Monroe 1970) and are direct evidence of subaerial unconformity. Grikes, while common in the peritidal facies association, are present in the ooid-shoal facies association at Sappington Canyon away laterally from the stratigraphic column, indicating these beds were also subaerially exposed. SB2 is present at Milligan Canyon and Crystal Lake. However, changes in bed geometries of the peritidal facies association at Milligan Canyon and discontinuous exposure at Crystal Lake made it difficult to place SB2 and overlying recrystallized grainstones into stratigraphic perspective.

Carbonate Point-Count Data

Fourteen different petrographic components have abundances greater than 5% of the total number of constituents within the eighty-one field samples (Fig. 7). Crinoidal grains are the most common component and are present in all 81 samples. Micrite is the next most common component (72 samples), followed by smooth (56 samples) and ribbed brachiopods (52 samples). While not as ubiquitous, other common components include spar (46 samples), indeterminant brachiopod fragments (43 samples), peloids (43 samples), and chert (31 samples). Less common components include pore space (17 samples), solitary corals (12 samples), algae (11 samples), fenestrate (eight samples) and trepostome (nine samples) bryozoans, and ooids (five samples).

Two-way cluster analysis of thin-section components identifies three distinct petrographic clusters among the 81 field samples (Fig. 7). The first cluster is crinoid-dominated, with crinoid abundances of 50% or greater, and micrite and ribbed, smooth, and indeterminate brachiopod fragments making up the next abundant common components. The crinoid-dominated cluster (45 samples) includes samples from the foreshoal (31 samples), deep-subtidal (13 samples), and ooid-shoal facies associations (one sample).

The second cluster includes samples that contain abundant peloids and crinoid grains, with smooth, ribbed, and indeterminate brachiopod fragments making up the next most common grains. This peloidal-crinoidal cluster (12 samples) includes samples from the foreshoal (8 samples) and deep-subtidal facies associations (four samples).

The third cluster includes samples that have abundant micrite and crinoid grains, with brachiopod fragments making up the next most common grains. This micritic-crinoidal cluster (24 samples) includes samples from the foreshoal (14 samples), deep-subtidal (nine samples), and ooid-shoal facies associations (one sample).

Depositional environments have similar frequencies of occurrence within the petrographic clusters identified in the two-way cluster analysis, indicating little correlation between lithological components and deposi-

Downloaded from http://pubs.geoscienceworld.org/sepm/palaios/article-pdf/36/3/95/5270967/i0883-1351-36-3-95.pdf

-

FIG. 6.—Stratigraphic cross section of the Lodgepole Formation and Allan Mountain Limestone. Black circles represent the stratigraphic position of field counts. Facies associations are abbreviated as follows: O = offshore; DS = deep subtidal; FS = foreshoal; OS = ooid shoal; CS = crinoid shoal; P = peritidal. Sequence-stratigraphic terminology is abbreviated as follows: SB = sequence boundary; ts = transgressive surface; mfz = maximum flooding zone; LST = lowstand systems tract; TST = transgressive systems tract; HST = highstand systems tract.



Fig. 7.—Two-way cluster analysis of thin-section point counts. The color of each cell represents the proportional abundance of a petrographic component within a sample. Samples are color-coded by depositional environment. Values < 5% of the total petrographic assemblage are not shown.

tional environment. Samples from the foreshoal facies association are dominant in the crinoid-dominated facies (69% of samples in facies), the peloidal-crinoidal (67% of samples in facies), and the micritic-crinoidal facies (58% of samples in facies). Samples from the deep-subtidal facies association are distributed at similar frequencies among the crinoid-dominated facies (29% of samples in facies), the peloidal-crinoidal cluster (33% of samples in facies), and the micritic-crinoidal facies (38% of samples in facies).

Faunal Data

Among the 81 samples, 2537 individuals from 84 species were counted. Solitary corals (10 species, 60% of individuals) and brachiopods (46 species, 28% of individuals) dominate the assemblages. Bryozoans (four species, 3% of individuals), colonial corals (four species, 1.5% of individuals), and gastropods (four species, 1.5% of individuals) are less common. Bivalves (four species), cephalopods (one species), and proetid trilobites (one species) are rare. Crinoids are present in all samples and include seven ossicle morphotaxa. Two crinoid species are identified with well-preserved calices and one calyx morphospecies from poorly preserved calices.

The culled species-abundance matrix reduced the original matrix to 2119 individuals and 20 species. Solitary corals dominate the culled dataset (seven species, 70% of culled individuals). Brachiopods from Rhynchonellata (seven species, 15% of culled individuals) and Strophomenata (two species, 7% of culled individuals) are the next most common groups, followed by the round crinoid ossicle morphotaxon (3% of culled individuals), elliptical individuals), elliptical



Fig. 8.—Two-way cluster analysis of faunal counts. The color of each cell represents the proportional abundance of a taxon in a sample. Samples are color-coded by depositional environment and taxa are color-coded by taxonomic class. Values < 1% the total faunal assemblage are not shown.

crinoid ossicle morphotaxon (1.5%) of culled individuals), and the trepostome bryozoan *Rhombopora* (1.5%) of culled individuals).

Two-way cluster analysis of the culled species-abundance matrix indicates two clusters (Fig. 8). The first cluster is the diverse brachiopod biofacies, dominated by the brachiopods *Schuchertella chemungensis* and *Spirifer centronatus*. Other common brachiopods include *Rhipidomella* sp. (15 samples), *Composita humilis* (11 samples), and *Camarotoechia* sp. (10 samples), but they are not ubiquitous across samples. Also common within this assemblage are round crinoid ossicles (26 samples) and the solitary corals *Cyathaxonia arcuata* (17 samples), *Zaphrentites* sp. (14 samples),

and *Rylstonia* sp. (11 samples). The diverse brachiopod biofacies is present in 18 deep-subtidal samples, 10 foreshoal samples, and no ooid-shoal samples.

The second cluster is the solitary coral-dominated biofacies, with *Cyathaxonia arcuata* (50 samples) and *Rylstonia* sp. (48 samples) being the most abundant solitary corals. Other common solitary corals include *Homalophyllites* sp. (35 samples), *Vesiculophyllum* sp. (25 samples), *Menophyllum* sp. (22 samples), and *Zaphrentites* sp. (21 samples). Round crinoid ossicles are also common within this biofacies (38 samples). Brachiopods are rarely identifiable to genus but include productids and



spiriferids. The solitary coral-dominated biofacies comprises samples predominantly from the foreshoal facies association (41 samples), but also includes some deep-subtidal (nine samples) and ooid-shoal (two samples).

Nonmetric Multidimensional Scaling

The NMS ordination plots samples and species such that samples close to one another are similar in composition, and species that plot close to one another tend to co-occur (Fig. 9A, 9B). The amount of explained variation decreases from axis 1 to axis 2, and so on. Coding the samples by depositional environment indicates an onshore-offshore gradient along NMS axis 1 (Fig. 9A). Samples grade from the deep-subtidal association in negative values of NMS axis 1 to the foreshoal association in positive values of NMS axis 1. Ooid-shoal samples plot with the foreshoal samples, indicating that their assemblage compositions are similar. Species also show a gradation along NMS axis 1, with brachiopods at negative values of NMS axis 1 and solitary corals at positive values (Fig. 9B). Samples from the deep-subtidal facies association are dominated by brachiopods, whereas the samples from the foreshoal facies association are dominated by solitary corals. The clustering of species and samples within the NMS ordination space is similar to biofacies clustering within the two-way cluster analysis, which also indicates the diverse brachiopod biofacies is predominantly samples from the deep-subtidal facies association and the solitary coral-dominated biofacies is predominantly samples from the foreshoal facies association (Fig. 8).

NMS axis 2 indicates greater variation in samples from the foreshoal facies association than the deep-subtidal facies association (Fig. 9A). Samples from the ooid-shoal facies association occur only at negative values of NMS axis 2 (Fig. 9A). Taxa indicate a gradation along NMS axis 2 when coded by class (Fig. 9B). Brachiopod taxa mostly cluster close together and centrally along NMS axis 2, although, the rhynchonellids *Nucleospira obesa* and *Atrypa* sp. are common at high positive NMS axis 2 values, and indeterminate productids plot at negative NMS axis 2 scores. Solitary corals clustering centrally along NMS axis 2 include *Amplexoccarina* sp., *Rylstonia* sp., *Cyathaxonia arcuata*, and *Vesiculophyllum* sp., whereas *Menophylum* sp., *Homalophyllites* sp., and *Zaphtentites* sp. are at negative values along NMS axis 2. Fenestrate bryozoans also are at negative NMS axis 2 scores.

The *envfit* correlation between ordination scores and lithological variables plots vectors in the ordination space where the length of the vector signifies the strength of relationship along a given axis (Fig. 9C). Ordination scores of the lithological variables are calculated for each axis of ordination (Table 2). Variables with large axis scores have a strong correlation with that axis. Positive scores on NMS axis 1 indicate samples rich in solitary coral (axis 1 score of 0.97) and peloid (axis 1 score of 0.89) constituents. Negative scores on NMS axis 1 indicate samples rich in micrite (axis 1 sore of -0.99) and trepostome bryozoan (axis 1 score of -0.90) constituents and grayer hue (axis 1 score of -0.88). Positive scores on NMS axis 2 indicate samples rich in smooth brachiopod (axis 2 score of 1.00) constituents. Negative scores on NMS axis 2 indicate samples rich in smooth brachiopod (axis 2 score of -0.96), spar (axis 2 score of -0.95), ooid constituents (axis 2 score of -0.94)

FIG. 9.—NMS ordination of sample-by-taxon matrix along axes 1 and 2. A) Samples coded by depositional environment. B) Taxa coded by taxonomic class. Only taxa with a proportional abundance greater than 1% are shown for clarity. See Table 3 for taxon codes. C) Ordination of environmental variables within the sample by taxon ordination space. The direction of the vector indicates its correlation with the NMS axis, and the length of the vector reflects the strength of the relationship. The names of species and lithological components, as well as the vectors of the environmental variables are rescaled such that names and arrows are more clearly visible.

TABLE 2.—Ordination scores for	lithological	variables.	Strong	loadings
(i.e., greater than 0.80 an	nd less than	-0.80) are	e in bold	!.

	NMS Axis 1	NMS Axis 2
Brachiopod indet.	0.60	-0.80
Ribbed brachiopod	-0.75	0.66
Smooth brachiopod	-0.04	1.00
Crinoid	0.29	-0.96
Fenestrate bryozoan	-0.66	-0.75
Trepostome bryozoan	-0.90	0.44
Solitary coral	0.97	0.26
Peloid	0.89	0.46
Ooid	-0.35	-0.94
Algae	0.62	-0.78
Micrite	-0.99	0.13
Pore space	0.64	0.77
Spar	-0.33	-0.95
Chert	0.74	-0.67
Bioturbation	0.07	-1.00
Munsell hue	-0.88	-0.47
Munsell value	-0.47	-0.88

and indeterminant brachiopod constituents (axis 2 score of -0.80) and have a lower value (axis 2 score of -0.88), indicating a lighter rock color.

DISCUSSION

Carbonate Facies Associations

The carbonate facies associations identified in the lower Madison Group are mostly congruent with those of Elrick and Read (1991), as well as Sonnenfeld (1996) and Smith et al. (2004). One major difference is that fewer lithofacies are recognized here than in previous studies. Elrick and Read (1991) identified 11 lithofacies across six facies associations and Sonnenfeld (1996) identified 16 lithofacies across five depositional environments, compared with the seven lithofacies across six depositional environments recognized here (Table 1). Sonnenfeld (1996) also included the upper Madison Group, which may record their greater number of lithofacies from the lagoonal and peritidal environments that dominate the upper Madison Group. The number of facies and environments identified are most similar to Smith et al. (2004), who identified seven lithofacies and depositional environments.

The offshore facies association in central Montana is comparable to the ramp-slope of Elrick and Read (1991) and outer ramp facies of Sonnenfeld (1996). All studies characterized this facies association as a carbonate mudstone interbedded with shale or argillite couplets deposited in a dysoxic to oxic environment below storm-wave base (Elrick and Read 1991; Sonnenfeld 1996). Elrick and Read (1991) also identified bryozoancrinoidal bioherms, interpreted as offshore carbonate mud mounds. These were identified at only one of their localities and may represent a more localized feature.

The deep-subtidal facies association is comparable to the deep ramp of Elrick and Read (1991) and middle ramp facies of Sonnenfeld (1996) and Smith et al. (2004). The bioturbated, skeletal packstone with argillaceous partings is interpreted as being deposited above storm-wave base and is common in all studies of the lower Madison Group with only subtle variations. Elrick and Read (1991) and Sonnenfeld (1996) all noticed graded bedding within their facies associations. Skeletal grains were denser along argillaceous partings, but actual grading within beds was not noticed in this study. Elrick and Read (1991) also included skeletal-ooid grainstone caps within their deep ramp facies association, based on the presence of hummocky cross-stratification, which commonly forms from storm activity (Aigner 1982; Dott and Bourgeois 1982; Duke 1985; Tucker and Wright

1990; Flügel 2010). Hummocky cross-stratification was not identified within any skeletal grainstone lithofacies of this study, and as a result, all skeletal-grainstones were interpreted as above fair-weather wave base.

The skeletal grainstone and carbonate mudstone lithofacies of the foreshoal facies association corresponds to the shallow subtidal of Elrick and Read (1991) and foreshoal-intershoal and bank of Smith et al. (2004) depositional environments. The skeletal grainstone represents localized reworking of skeletal grains to form the shoal and bank deposits (Elrick and Read 1991; Smith et al. 2004) with cross-stratification identified in previous studies suggesting a high shear stress environment. No crossstratification was identified within the skeletal grainstone lithofacies but was presumably destroyed by bioturbation. The carbonate mudstones are interpreted as more protected intershoal deposits where fossils and skeletal grains are inferred to be a mixture of autochthonous material and those transported from adjacent shoal and bank deposits (Elrick and Read 1991; Smith et al. 2004). Foreshoal bank-intershoal complexes are found in other Mississippian carbonate ramps (Carr 1973; Smith and Read 1999, 2001; Burrowes 2006; Bonelli and Patzkowsky 2008) as well as in modern carbonate environments (Hine 1977; Read 1985; Tucker and Wright 1990; Burchette and Wright 1992; Flügel 2010).

Ooid-shoal facies are identified in all previous studies of the lower Madison Group (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004), as are thick cycles of ooid-shoal facies, which were also observed in the HST of this study. Ooid-shoals in modern settings such as the Bahamas and the Persian Gulf form within warm, shallow water that experience strong tidal currents and waves (Ball 1967; Hine 1977; Harris 1979; Halley et al. 1983; Wanless and Tedesco 1993), supporting the tropical setting of the lower Madison Group during the Mississippian (McKerrow and Scotese 1990). Ooid shoals are typically poorly fossiliferous, sedimentmobile environments (Feldman et al. 1993), which matches the low diversity and abundance of fossils observed in this study.

The crinoid-shoal facies association is interpreted as lagoonal by Elrick and Read (1991) and Smith et al. (2004) or as another sub-environment of the foreshoal by Elrick and Read (1991) depending on its stratigraphic context. If it appears stratigraphically below the ooid shoals, crinoidal grainstones can be interpreted as foreshoal facies, and if it appears above the ooid shoal it is lagoonal (Elrick and Read 1991). In this study, the crinoid-shoal facies association appears above the ooid-shoal facies association in shallowing-upward parasequences, indicating it represents a lagoonal depositional environment. Further evidence supporting a lagoonal interpretation is lack of cross-stratification that would be expected in the foreshoal (Elrick and Read 1991; Smith et al. 2004). The low diversity and abundance of fossils also support more restricted conditions. The light tan color of this facies association is also evident in the Madison Shelf (Elrick and Read 1991; Smith et al. 2004), suggesting that this facies was commonly dolomitized (Tucker and Wright 1990; Flügel 2010) across the entire shelf. While bacterially mediated synsedimentary dolomitization. seawater reflux, and seawater dolomitization are common in shallow water carbonates (Tucker and Wright 1990; Melim and Scholle 2002; Machel 2004; Flügel 2010; Meister et al. 2013), the exact mode of dolomitization for the crinoid-shoal facies association cannot be determined without further petrographic and geochemical analyses.

The peritidal facies association is similar to that of previous studies (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). Planarlaminated carbonate mudstones interbedded with structureless carbonate mudstones indicate a quiet water, restricted lagoonal to supratidal environment (Elrick and Read 1991; Tucker and Wright 1990; Sonnenfeld 1996; Smith et al. 2004). Laminations are likely caused by algal mats living on the sediment surface (Elrick and Read 1991; Smith et al. 2004) that trap and bind the sediment (Tucker and Wright 1990; Flügel 2010). In addition to the grikes observed in this study, this facies association commonly contains brecciation and other karst features where exposed beneath sequence boundaries on the Madison Shelf (Elrick and Read 1991; Sonnenfeld 1996; Smith et al 2004), indicating the presence of a subaerial unconformity.

Sequence-Stratigraphic Architecture

One third-order depositional sequence (*sensu* Van Wagoner et al. 1988) for the lower Madison Group is identified at the four localities in central Montana. The interval between the lower sequence boundary (SB1) at the unconformity with the Sappington Formation and the upper sequence boundary (SB2) at the contact with the upper Madison Group spans approximately 4 million years (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). Previous studies of the lower Madison group identified two (Sonnenfeld 1996; Smith et al. 2004) or three (Elrick and Read 1991) third-order depositional sequences during the same interval.

One possibility for the difference in the number of sequences is that three of the columns measured for this study represent the more distal Central Montana Trough (Fig. 1) where the sequence boundaries of the more proximal Madison Shelf are not easily distinguishable (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). In fact, Elrick and Read (1991) could not confidently extend the sequence boundary overlying their second sequence up-dip into central Wyoming, owing to lack of change in stacking patterns, and they combined the sequence boundary with a flooding surface down-depositional dip into central Montana. Additional measured sections within the Central Montana and along the northwestern shelf near the Gibson Reservoir locality would provide the information necessary to identify changes in stacking patterns that can be correlated to sequence boundaries on Madison Shelf.

The second possibility for this difference is the different approaches in defining sequence boundaries. Following Elrick and Read (1991), I apply the Van Wagoner et al. (1988) model of placing sequence boundaries at unconformities separating the HST and from the overlying LST where stacking patterns transition from progradational stacking patterns to aggradational stacking patterns and are typically associated with subaerial exposure. Sonnenfeld (1996) and Smith et al. (2004) use transitions from decreasing accommodation cycles (i.e., regressive) to increasing accommodation cycles (i.e., regressive) to increasing accommodation cycles (i.e., transgressive) to demarcate sequence boundaries and not changes in progradational stacking or subaerial unconformities (cf. Embry and Johannessen 1992). This may account for discrepancies between this study and Sonnenfeld (1996). It does not explain the differing number of depositional sequences between this study and Elrick and Read (1991), which is better explained by the failure to identify the correlative conformities of Elrick and Read (1991).

The position of SB1 at the basal contact with the Sappington Formation corresponds with the lowest sequence boundary of the first depositional sequence of Elrick and Read (1991), Sonnenfeld (1996), and Smith et al. (2004). The position of SB2 at the upper contact with the Mission Canyon Formation and Castle Reef Dolomite of the upper Madison Group corresponds to the upper sequence boundaries of the second depositional sequence of Sonnenfeld (1996) and Smith et al. (2004) and with the upper sequence boundary of the third depositional sequence of Elrick and Read (1991). Thus, although all studies agree that there is a sequence boundary at the base and top of the Lodgepole Formation, they disagree on whether the Lodgepole Formation contains any unconformities.

While carbonate facies associations differ between the more distal Central Montana Trough (i.e., this study) and the more proximal Madison Shelf (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004), stacking patterns of parasequences allow for comparison of systems tract architecture. The LST in this study is defined similarly to Elrick and Read (1991), with parasequences grading from progradationally stacked to aggradationally stacked. Neither Sonnenfeld (1996) nor Smith et al. (2004) recognize an LST in their sequences as they place progradationally stacked packages into their HST and aggradationally stacked packages into their TST.

The TST in this study is defined identically with Elrick and Read (1991) and similar to Sonnenfeld (1996) and Smith et al. (2004), where all retrogradationally stacked parasequences are placed within the TST. Sonnenfeld (1996) and Smith et al. (2004) include all aggradationally stacked parasequences within the TST.

The HST in this study is defined similarly to Elrick and Read (1991) with parasequences grading from aggradationally stacked to progradationally stacked. The HST in this study differs from Sonnenfeld (1996) and Smith et al. (2004) as those studies considered only progradationally stacked parasequences that also binned portions of the LST within their HST.

As I identified only one third-order depositional sequence, the systems tracts in this study do not match those identified by Elrick and Read (1991), Sonnenfeld (1996), and Smith et al. (2004). The position of the TST and HST of this study may correlate however with the TST and HST of the third-order composite sequence of Sonnenfeld (1996) that examines more long-term trends in accommodation history within the lower Madison Group.

The boundary between the TST and HST at the four central Montana localities in this study is marked by the furthest landward progression of the deepest carbonate facies association. While an individual maximum flooding surface could not be identified, a several meter interval signifying the presence of the deepest water faces known as a maximum flooding zone is present at all localities. Sonnenfeld (1996) also used maximum flooding zones to distinguish the boundary between their TST and HST along the Madison Shelf. Elrick and Read (1991) discuss the difficulty of correlating a single maximum flooding surface across along the Madison Shelf, and apply the maximum flooding zone approach for their second and third depositional sequences. Assuming the TST and HST of this study correlates to the TST and HST of the third-order composite sequence of Sonnenfeld (1996), the maximum flooding zone correlated among Sappington Canyon, Milligan Canyon, Crystal Lake, and Gibson Reservoir is equivalent to the maximum flooding zone of the lowermost third-order depositional sequence along the Madison Shelf (Elrick and Read 1991; Sonnenfeld 1996; Smith et al. 2004). This implies that the HST of this study incorporates not only the HST of the lowermost third-order sequence but also the remaining third-order sequences of the lower Madison Group. Future studies should examine these beds in the HST to identify additional sequence boundaries or correlative conformities for better correlations with the sequence-architecture established on the Madison Shelf (Mudge et al. 1962; Reid and Dorobek 1993).

Lithologic Variations

Crinoid ossicles are the predominant skeletal grain in these samples, and are abundant in all depositional environments, which is common in Mississispipan carbonate rocks (Ausich 1997; Kammer and Ausich 2006). Crinoids reached their peak abundance and diversity during the Tournaisian and Visean (Kammer and Ausich 2006), and dispersed themselves through a wide range of water depths, substrates, and wave energies (Kammer and Ausich 1987; Kammer et al. 1997, 1998; Kammer and Ausich 2006). Camerate crinoids are especially common in carbonate facies and are one of the most diverse group during the Mississippian (Kammer and Ausich 2006). Camerates are particularly diverse and abundant within the lower Madison Group (Laudon and Severson 1953; Laudon 1967), but the syntaxial cement surrounding most crinoid grains made taxonomic identification impossible in thin section.

The foreshoal and deep-subtidal samples of the crinoidal-dominated association (Fig. 7) are encrinites, carbonate rocks with compositions at least 50% crinoid grains (Ausich 1997; Kammer and Ausich 2006). Encrinites from the Mississippian form thick, regional deposits and are found in North America, Europe, the Middle East, and Asia (Waters and Sevastopulo 1984; Chen and Yao 1993; Ausich 1999a, 1999b; Webster et

al. 2003; Debout and Denayer 2018). While not true encrinites, the peloidal and micritic point-count clusters (Fig. 7) are also rich in crinoid grains, pointing to the dominance of crinoids during the Mississippian. The presence of thick, crinoidal deposits in the lower Madison Group indicates that open-marine stenohaline conditions were prevalent in Montana during the Mississippian, similar to other coeval carbonate ramps in North America and Europe (Kammer and Ausich 2006).

The presence of micrite-rich petrographic clusters within deep-subtidal and foreshoal samples is consistent with the facies model of Elrick and Read (1991) and Sonnenfeld (1996), who both reported carbonate wackestone with these facies associations. Micrite is produced in highenergy and low-energy environments of the carbonate factory, but its accumulation is determined by production rate, proximity to micrite source, and how quickly the micrite can be deposited and bound before it can be transported (Tucker and Wright 1990; Flügel 2010). Packstones in the deep subtidal generally have a high percentage of micritic matrix, as the deep subtidal is a location of micrite production as well as a recipient of micrite from shallower environments. Additionally, the deep subtidal experiences less frequent wave action to transport the micrite away as it is below fair-weather wave base (Tucker and Wright 1990; Flügel 2010). The foreshoal samples in this micritic-crinoidal association are sampled primarily from the carbonate mudstone lithofacies of intershoal environment (Table 1), which is also a location of micrite production, a recipient of micrite from adjacent shoals and banks, and protected from waves by the shoals and skeletal banks of the foreshoal facies association, similar to lagoons behind barrier islands and reefs (Tucker and Ward 1990; Flügel 2010).

Peloids are common in many samples from the deep subtidal and foreshoal, and they are a defining attribute of the third petrographic cluster (Fig. 7). Peloids are identified in these facies by Sonnenfeld (1996) and Smith et al. (2004). Peloids are also common in the lithofacies model established by Elrick and Read (1991), although they called them pellets. The term "pellets" indicates the fecal matter of a macrophagous detrital feeder (Flügel 2010), but pellets and non-fecal peloids in this study could not be distinguished, as is generally true (Tucker and Wright 1990; Flügel 2010). The large abundance of peloids likely indicates the presence of macrophagous detrital feeders such as gastropods or polychaete worms (Shinn 1968; Garrett 1977; Wanless et al. 1981; Tucker and Wright 1990; Flügel 2010), which are common detrital feeders in tropical, highly bioturbated carbonates (Flügel 2010) such as the lower Madison Group. Peloids can also be created from small fragments of micritized bioclasts (Bathurst 1975; Reid et al. 1992; Reid and MacIntyre 1998). This is equally plausible as whole and coarse skeletal grains (i.e., shell fragments greater than 2 mm) are partially or completely micritized when viewed in thin section.

Faunal Variations and Environmental Gradients

Faunal variation in the lower Madison Group is primarily correlated with water depth (Figs. 8, 9A). The two-way faunal cluster analysis indicates that the high-diversity brachiopod biofacies includes samples predominantly from the deep-subtidal facies association, whereas the solitary coral biofacies is predominantly found in the foreshoal facies association (Fig. 8). NMS axis 1 mirrors these results with samples grading from the deep subtidal to the foreshoal (Fig. 9A), and with taxa grading from brachiopod to solitary coral dominated (Fig. 9B). The lithological data is also consistent with a water-depth gradient. Samples grade along NMS axis 1 from an increased amount of micrite and bryozoan fragments to samples rich in peloids and coral fragments. While micrite is produced through a variety of mechanisms within most environments of a carbonate ramp, micrite-rich samples are typically interpreted as lower energy environments, such as lagoons, the deep subtidal, and offshore (Tucker and Wright 1990; Flügel 2010). Additionally, bryozoans are mostly identified in

assemblages from the deep subtidal and are only identified in thin sections of skeletal packstone samples.

As water depth is a complex gradient (*sensu* Whittaker 1956; Austin et al. 1984), it is far more likely that taxa responded to several of the many covarying variables (i.e., substrate, wave energy, temperature, oxygenation, nutrients) that contribute to the water-depth gradient than they did to water depth itself (Tait and Dipper 1998; Patzkowsky and Holland 2012). Taxa morphology, life habits, and ecology can provide clues to which of the covarying environmental variables are correlated with assemblage variation (see Lafferty et al. 1994; Patzkowsky 1995; Holland et al. 2001; Olszewski and Patzkowsky 2001; Webber 2002; Scarponi and Kowalewski 2004; Tomašových 2006; Redman et al. 2007; Perera and Stigall 2018).

Examining the distribution of brachiopod life mode within the NMS shows no relationship to the water-depth gradient. Brachiopods in the deep-subtidal facies association are predominantly rhynchonellids, which are pedunculate epifauna inferred to attach to the substrate surface (Rudwick 1970; Fürsich and Hurst 1974). Brachiopods in the foreshoal facies association are predominantly spiriferids, which are also pedunculate epifauna, and productids, which are sessile taxa with ornamentation adapted for resting on or semi-infaunally within soft substrates (Rudwick 1970; Fürsich and Hurst 1974). Typically, soft substrate environments commonly contain infaunal, semi-infaunal or resting epifaunal taxa (Rudwick 1970; Fürsich and Hurst 1974; Holland et al. 2001; Tomašových 2006; Perera and Stigall 2018). The ubiquitous distribution of pedunculate brachiopods indicates firm substrates may have been common in all facies associations within the lower Madison Group.

The occurrence of rugose corals may indicate a substrate gradient that covaries with water depth. Paleozoic rugose corals are found in a wide range of water depths but are more abundant and diverse in shallow waters (Sando 1980; Scrutton 1998). Most solitary corals live a liberosessile lifestyle in which they rest epifaunally on or semi-infaunally in the substrate (Elias et al. 1988; Bolton and Driese 1990; Scrutton 1998). Substrate composition and firmness, however, affect the hydrodynamic stability of rugose corals (Bolton and Driese 1990). Rugose corals resting on muddy substrates are often found in hydrodynamically unstable positions, whereas those resting on less muddy or firmer substrates are in more stable positions (Bolton and Driese 1990). The distribution of rugose corals in these assemblages is consistent with Mississippian and Paleozoic rugose coral ecology. Rugose corals in the lower Madison Group are present in the muddy skeletal packstone of the deep-subtidal facies association and carbonate mudstone lithofacies of the foreshoal facies associations. However, their increased diversity and dominance in the skeletal grainstone lithofacies of the foreshoal facies association coincides with a decrease in micrite (Fig. 9B, 9C). This decrease in micrite and muddy substrate may have led to more hydrodynamically stable rugose corals and increased survival (Bolton and Driese 1990).

Brachiopod ornamentation and rugose coral orientation also suggest wave energy may have covaried with water depth, as is expected on carbonate ramps (Read 1985; Burchette and Wright 1992). Brachiopods in the deep subtidal are predominantly smooth or fine-ribbed, suggesting quiet-water environments (Rudwick 1970; Fürsich and Hurst 1974). The presence of the coarse-ribbed Camarotoechia sp. as well as pedunculate rhynchonellids within the deep-subtidal facies associations may indicate the occurrence of strong waves produced by storms (Rudwick 1970; Fürsich and Hurst 1974). Rugose corals in the deep-subtidal facies association are commonly preserved in a vertical orientation with calices opening upwards and apices pointed downwards with respect to bedding surfaces. Rugose corals in the skeletal grainstone lithofacies of the foreshoal association are preserved oblique and on their sides with respect to the bedding surface, a position implying frequent wave action (Elias et al. 1988). Such differences in orientation suggest an increase in wave energy from the deep subtidal to the foreshoal (Elias et al. 1988).

Lithological data suggests that NMS axis 2 represents an oxygen gradient. Bioturbation, Munsell hue, and Munsell value are all highly correlated along NMS axis 2 (Table 2, Fig. 9C). As NMS axis 2 scores become more negative, Munsell hues and values indicate that rock color grades from brownish-dark gray to medium-light gray carbonate rocks. Color is commonly used as a qualitative assessment of redox state and oxygenation, with darker colors representing relatively carbon-rich, reduced conditions and lighter colors representing more carbon-poor and oxic conditions (Berner 1981; Maynard 1982; Savrda et al. 1984; Algeo and Maynard 2004; Piper and Calvert 2009). Incorporating Munsell hues and values into the multivariate analysis allows a qualitative variable to be transformed into a quantitative one to track gradational changes in color and oxidation.

In addition to a lightening in color, ichnofabric indices increases as NMS axis 2 becomes more negative, indicating greater vertical burrowing in the sediment surface (Droser and Bottjer 1986). Variations in vertical bioturbation are commonly controlled by oxygenation, substrate consistency, sedimentation rate, and nutrient levels (Shroud and Levin 1976; Wetzel and Uchman 1998; Taylor et al 2003; Martin 2004; Aguirre et al. 2010; Boyer and Droser 2011). However, it is unlikely that substrate consistency, sedimentation rate, or nutrient levels are contributing to the changes in bioturbation intensity observed in the lower Madison Group. Different burrowing structures are preserved in hard, muddy, or sandy substrates (Taylor et al. 2003). However, large vertical burrows with similar morphologies (e.g., Thalassinoides) are present in the deep subtidal and the foreshoal facies association despite the lithological differences. Additionally, the bioturbation gradient along NMS axis 2 is orthogonal to the substrate gradient along NMS axis 1 (Fig. 9C), which indicates bioturbation is independent of substrate. Decreasing sedimentation rates increases bioturbation intensity within the sediment (Shroud and Levin 1976; Taylor et al. 2003). Estimated rates of sedimentation for the lower Madison Group are 0.15-0.3 m/kyr for the deep subtidal facies association and 0.3-1.0 m/kyr for the foreshoal facies association (Elrick and Read 1991), which implies the greatest difference in sedimentation rates occurs along the onshore-offshore gradient on NMS axis 1. Samples from the deep subtidal and foreshoal facies association all demonstrate an increase in bioturbation along NMS axis 2 despite their different sedimentation rates, suggesting that changes in sedimentation rate are unlikely to be influencing bioturbation. Increasing nutrient levels can also increase bioturbation intensity, especially in environments with high sedimentation rates (Wetzel and Uchman 1988; Taylor et al. 2003). However, increased nutrient levels is commonly associated with darker rock colors (i.e., dark brown, dark green, and black; Wetzel and Uchman 1988; Taylor et al. 2003). The vectors of the lithological data within the NMS indicates that rock color transitions from dark gray to light gray as bioturbation increases along NMS axis 2 (Fig. 9C), which suggests that an increase in nutrients is not driving the increased bioturbation. As neither substrate consistency, nor sedimentation rate, nor nutrient levels appear to explain the increase in bioturbation intensity, and since bioturbation increases as rock color transitions from dark to light gray, an oxygenation gradient is the mostly likely environmental variable explaining the faunal and lithological variation within the lower Madison Group along NMS axis 2. If NMS axis 2 represents oxygen, it implies that the brachiopods Nucleospira obesa and Atrypa sp. prefer settings with more reduced pore-water conditions, whereas solitary corals in the lower Madison Group prefer settings with well-oxygenated pore waters (Fig. 9B).

Biogenic structures indicate that oxygenation levels for all samples range from slightly dysaerobic to fully aerobic. Seventy-eight of the 81 samples have ichnofabric indices ranging from ii3–ii5 indicating moderate to heavy levels of bioturbation intensity all depositional environments (*sensu* Droser and Bottjer 1986). Only three samples from the foreshore facies association have an ichnofabric index of ii2. This suggests that aerobic conditions were prevalent within the deep subtidal, foreshoal, and

ooid shoal facies associations (sensu Boyer and Droser 2011), and that the oxygen gradient is independent and uncorrelated with the water-depth gradient. Additionally, multiple, large burrow structures such as Thalassinoides are common in the deep-subtidal and the foreshoal associations, which also indicates aerobic bottom was common across all depths (Boyer and Droser 2011). Zoophycos, Taenadium? and other horizontal feeding traces are identified only in the deep-subtidal facies association and variations in abundance may indicate occasional fluctuations in oxygenation, sedimentation rate, and nutrient supply in more distal facies (Shroud and Levin 1976; Wetzel and Uchman 1998; Taylor et al. 2003; Martin 2004; Aguirre et al. 2010; Boyer and Droser 2011). Tiering of ichnofossils can also provide clues to changes in bottom and pore-water oxygenation during deposition (Bromley and Eckdale 1986; Savrda and Bottjer 1986; Taylor et al. 2003; Savrda 2007). Unfortunately, most beds sampled for faunal counts were heavily bioturbated, obscuring any distinct burrows and trace fossils within the beds and making it difficult to use ichnofossil tiering to assess changes in oxygenation for the lower Madison Group. Based on the heavy bioturbation of sampled beds and presence of deep burrows in the deep subtidal and foreshoal facies association, it is reasonable to infer that these facies experienced aerobic conditions at time of deposition. Finally, the absence of authigenic minerals in the point-count data, with the exception of glauconite as rare constituents in two samples from Sappington Canyon, provides additional support for aerobic pore waters within the lower Madison Group.

Implications

This high-resolution gradient analysis of the lower Madison Group demonstrates the importance of combining lithological and faunal data when analyzing ancient communities. Coding samples and taxa by lithology within the ordination space is already a common technique for multivariate analyses (e.g., Patzkowsky 1995; Holland et al. 2001; Bush and Brame 2010; Hendy 2013; McMullen et al. 2014; Zuschin et al. 2014; see Patzkowsky and Holland 2012 for review). However, lithological characters are often derived from the facies-level descriptions that are used to broadly define depositional environments. While this method is still very useful (Patzkowsky and Holland 2012), it does not account for any heterogeneity between lithologic beds, similar to the heterogeneity in shell beds (Bennington 2003; Webber 2005), and that specific beds or bedsets might preserve slight variations in environmental conditions. I expand upon these established techniques by directly quantifying lithological variables associated with each faunal count, and directly overlaying this information within the same ordination space. This allowed for more indepth descriptions of how lithology is changing within and among depositional environments as well as along water depth and substrate gradients. While I applied the envfit function to only an NMS, the envfit function is flexible enough to be used with the other ordination techniques common in community analysis (e.g., detrended correspondence analysis, correspondence analysis; Oksanen et al. 2019). Constrained ordinations such as canonical correspondence analysis are an additional method to interpret species abundance data within the context of environmental data, and although these techniques are best suited for testing correlations with specific environmental variables, they can still be useful in gradient exploration (ter Brakk 1986; McCune and Grace 2002). Regardless of the technique used, ordinations that include quantifiable lithological and environmental variables for each faunal sample improve the visualization of potential gradients, aid in the description of covarying gradients, and strengthen the interpretation of gradients along ordination axes.

Ecological characteristics of taxa (e.g., life habit, feeding mode, morphology, and ecological preferences) are also commonly overlain on to taxonomic distributions within multivariate analyses to further define environmental gradients. These ecological characters have been implemented in tandem with lithological data (e.g., Scarponi and Kowalewski TABLE 3.—Taxonomic codes for the NMS ordination (Fig. 9).

Species	Code
Amplexocarina sp.	Amc
Atrypa sp.	Atr
Camarotoechia sp.	Cam
Composita humilis	Com
Cyathaxonia arcuata	Суа
Elliptical crinoid ossicle	Ecr
Fenestrate bryozoan	Fen
Homalophyllites sp.	Hom
Menophyllum sp.	Men
Nucleospira obesa	Nuc
Productid indeterminate	Pro
Rhipidomella sp.	Rhi
Rylstonia sp.	Ryl
Schuchertella chemungensis	Sch
Spiriferid indeterminate	Sp
Spirifer centronatus	Spc
Vesiculophyllum sp.	Ves
Zaphrentites sp.	Zap

2004; Redman et al. 2007; Amorosi et al. 2014; Perera and Stigall 2018), and also when taxonomic changes are not correlated with changes in lithological data (e.g., Kowalewski et al. 2002; Lebold and Kammer 2006; Bush and Brame 2010; Hendy 2013; Zuschin et al. 2014). This study reenforces the utility of ecological characteristics to assist in interpreting environmental gradients. The distribution of solitary corals within the lower Madison Group suggest that the diversity, abundance, and dominance of specific taxonomic groups are additional potential ecological characteristics to assist in defining environmental gradients, something observed in previous ordinations of ancient benthic communities (Erwin 1989; Lafferty et al. 1994; Dineen et al. 2013). Variations in the preservation of these solitary corals also suggest that combining shell orientation and other taphonomic variables with lithological data is useful in interpreting environmental gradients (e.g., hydrodynamic stability and wave energy) within ancient communities, similar to the use of shell morphology and structure (Bush and Brame 2010; Zuschin et al. 2014).

Lastly, this study emphasizes the importance of including lithological data for each faunal count when defining secondary environmental gradients. Traditional methods of facies-level lithological descriptions can leave higher axes of ordination un-interpreted and therefore any secondary gradients go unreported (e.g., Cisne and Rabe 1978; Patzkowsky 1995; Olszewski and Patzkowsky 2001; Webber 2002; Tomašových 2006; Redman et al. 2007; Amorosi et al. 2014; Scarponi et al. 2014; Foster et al. 2015; Perera and Stigall 2018). The lithological and faunal variation within the lower Madison Group demonstrates how direct sampling of lithological and faunal samples together and their inclusion within the same multivariate analyses can provide an avenue to explore these additional gradients. Standard facies-level descriptions could only identify a water depth and substrate as the primary environmental gradients for the lower Madison Group. Oxygenation as a secondary gradient controlling faunal variation was only identifiable by quantifying the petrographic components, bioturbation index and intensity, and rock color for each faunal sample, and then analyzing the ordination of faunal samples within the context of changes in these lithological variables. Combining closely spaced, replicate sampling of both lithological and faunal data is crucial to uncovering the underlying environmental gradients preserved in the lithological record and interpreting their impacts on community compositions in the fossil record.

CONCLUSIONS

A total of six carbonate facies associations and seven depositional environments are identified in the lower Madison Group at the four localities in this study. While fewer lithofacies are identified in this study compared with previous studies of the Madison Group, patterns between carbonate facies associations and depositional environment are consistent between studies.

One third-order depositional sequence is identified for the lower Madison Group within the Central Montana Trough and on the northwestern shelf, which differs from the two or three third-order depositional cycles identified to the southwest along the Madison Shelf. The third-order depositional sequence identified here is likely a composite sequence that incorporates the same timeframe of the previously identified sequences on the Madison Shelf.

The two-way cluster analysis of petrographic components identifies three petrographic clusters within the lower Madison Group in central Montana: crinoid dominated, peloid-crinoid, and micrite-crinoid. These groupings do not correlate with lithological facies associations nor do they correlate with an onshore-offshore gradient. Lithological variations are consistent with lithologic patterns along the Madison Shelf to the south as well as other carbonate ramp systems in the Mississippian.

The two-way cluster analysis of faunal data identifies two biofacies. The diverse brachiopod biofacies is dominated by *Schuchertella chemungensis* and *Spirifer centronatus*, and it includes samples predominantly from the deep-subtidal facies association as well as samples from the carbonate mudstone lithofacies of the foreshoal facies association. The solitary coral-dominated biofacies is dominated by *Cyathaxonia arcuata* and *Rylstonia* sp., and it includes samples predominantly from the foreshoal facies association.

Water depth is the primary gradient associated with variation in faunal assemblages along NMS axis 1. Deep-subtidal assemblages are defined by the diverse brachiopod biofacies and foreshoal assemblages are defined by a rugose coral-dominated assemblage. The carbonate facies associations, biofacies and lithological data grade along the first axis of ordination in relation to the onshore-offshore gradient, indicating a transition to less muddy and higher energy conditions more proximal to shore.

Ordinating the lithological data within the NMS of the faunal data identifies a secondary oxygen gradient potentially associated with faunal variation reflected by increase in bioturbation and a lightening of rock color. Samples from the foreshoal association display greater variation along NMS axis 2. Distribution of species along NMS axis 2 indicate the brachiopods *Nucleospira obesa* and *Atrypa* sp. are more abundant in settings with reduced, pore-water conditions whereas solitary corals prefer settings with more oxygenated pore waters.

This study demonstrates the efficacy of directly linking lithological data to faunal data when conducting ecological analyses. Combining closely spaced, replicate sampling of lithological data in conjunction with faunal data unlocks additional sources of environmental variation driving fossil assemblage compositions, providing more detailed environmental reconstructions and understanding of community compositions in the fossil record.

ACKNOWLEDGMENTS

I am grateful to T. Rice, P. Monarrez, and J. Slattery for their assistance in the field. I am also grateful to B. Douglas, M. Toensing, and the rest of the faculty and staff at the Indiana University Judson Mead Geological Field Station for housing, logistical support, and assistance with accessing field sites on private lands. I would like to thank S. Holland, S. Goldstein, J. Byers, M. Kowalewski, and M. Patzkowsky for their helpful comments and constructive suggestions on early versions of this manuscript. Finally, I would like to thank E. Jarochoska, V. Roden, and an anonymous reviewer for their helpful comments that improved this manuscript. Funding for this project was provided by the Indiana University

Judson Mead Geologic Field Station Charles J. Vitaliano Grant in Aid, Geological Society of America Student Research Grant, the Tobacco Root Geological Society, the Wyoming Geological Association, the Gilles and Bernadette Allard Geology Award, and the Mirriam Watts-Wheeler Fund.

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: https://www.sepm.org/supplemental-materials.

REFERENCES

- AGUIRRE, J., DE GIBERT, J.M., AND PUGA-BERNABÉU, A., 2010, Proximal-distal ichnofabric changes in a siliciclastic shelf, Early Pliocene, Guadalquivir Basin, southwest Spain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 291, p. 328–337.
- AIGNER, T., 1982, Calcareous tempestites: storm-dominated stratification, Upper Muschelkalk limestones (Middle Triassic, SW-Germany), in G. Einsele and A. Seilacher (eds.), Cyclic and Event Stratigraphy: Springer, Berlin, p. 180–198.
- ALGEO, T.J. AND MAYNARD, J.B., 2004, Trace-element behavior and redox facies in core shales of Upper Pennsylvanian Kansas-type cyclothems: Chemical Geology, v. 206, p. 289–318.
- AMOROSI, A., ROSSI, V., SCARPONI, D., VALANI, S.C., AND GHOSH, A., 2014, Biosedimentary record of postglacial coastal dynamics: high-resolution sequence stratigraphy from the norther Tuscan coast (Italy): Boreas, v. 43, p. 939–954.
- ANDRICHUK, J.M., 1955, Mississippian Madison Group stratigraphy and sedimentation in Wyoming and Southern Montana: American Association of Petroleum Geologists Bulletin, v. 39, p. 2170–2210.
- AUSICH, W.I., 1997, Regional encrinites: a vanished lithofacies, *in* C.E. Brett and G.C. Baird (eds.), Paleontological Events: Stratigraphic, Ecologic and Evolutionary Implications: Colombia University Press, New York, p. 509–519.
- AUSICH, W.I., 1999a, Lower Mississippian Hampton Formation at LeGrand, Iowa, USA, *in* W.I. Ausich, C.E. Brett, H. Hess, and M.J. Simms (eds.), Fossil Crinoids: Cambridge University Press, Cambridge, p. 135–138.
- AUSICH, W.I., 1999b, Lower Mississippian Burlington Limestone along the Mississippi River Valley in Iowa, Illinois, and Missouri, USA; *in* W.I. Ausich, C.E. Brett, H. Hess, and M.J. Simms (eds.), Fossil Crinoids: Cambridge University Press, Cambridge, p. 139–144.
- AUSTIN, M.P., CUNNINGHAM, R.B., AND FLEMING, P.M., 1984, New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures: Vegetatio, v. 55, p. 11–27.
- BALL, M.M., 1967, Carbonate sand bodies of Florida and The Bahamas: Journal of Sedimentary Petrology, v. 37, p. 556–591.
- BATHURST, R.G.C., 1975, Carbonate Sediments and Their Diagenesis: Elsevier, Amsterdam, p. 658.
- BENNINGTON, J.B., 2003, Transcending patchiness in the comparative analysis of paleocommunities: a test case from the Upper Cretaceous of New Jersey: PALAIOS, v. 18, p. 22–33.
- BERNER, R.A., 1981, A new geochemical classification of sedimentary environments: Journal of Sedimentary Petrology, v. 51, p. 359–365.
- BOLTON J.C. AND DRIESE, S.G., 1990, The determination of substrate conditions from the orientations of solitary rugose corals: PALAIOS, v. 5, p. 479–483.
- BONELLI, J.R. AND PATZKOWSKY, M.E., 2008, How are global patterns of faunal turnover expressed at regional scales? Evidence from the Upper Mississippian (Chesterian Series), Illinois Basin, USA: PALAIOS, v. 23, p. 760–772.
- BOYER, D.L. AND DROSER, M.L, 2011, A combined trace- and body-fossil approach reveals high-resolution record of oxygen fluctuations in Devonian seas: PALAIOS, v. 26, p. 500–508.
- BROMLEY, G.G. AND ECKDALE, A.A., 1986, Composite ichnofabrics and tiering of burrows: Geological Magazine, v. 231, p. 59–65.
- BURCHETTE, T.P. AND WRIGHT, V.P., 1992, Carbonate ramp depositional systems: Sedimentary Geology, v. 79, p. 3–57.
- BURROWES, G., 2006, Genesis of Mississippian shoal topography, Weyburn Field, Saskatchewan, *in* E.H. Nickel (ed.), Saskatchewan and Northern Plains Oil and Gas Symposium Core Workshop Volume: Saskatchewan Geological Society Special Publication, v. 20, p. 22–31.
- BUSH, A.M. AND BRAME, R.I., 2010, Multiple paleoecological controls on the composition of marine fossil assemblages from the Frasnian (Late Devonian) of Virginia, with a comparison of ordination methods: Paleobiology, v. 36, p. 573–591.
- CARR, D.E., 1973, Geometry and origin of oolite bodies in the Ste. Genevieve Limestone (Mississippian) in the Illinois Basin: Indiana Geological Survey Bulletin, v. 48, p. 1–81.
- CHEN, X. AND WEBSTER, G.D., 1994, Sedimentology, tectonic control and evolution of a Lower Mississippian carbonate ramp with offshore bank, central Wyoming to eastern Idaho and northeastern Utah, U.S.A., *in* A.F. Embry, B. Beauchamp, and D.J. Glass (eds.), Pangea: Global Environments and Resources: Canadian Society of Petroleum Geologists Memoir, v. 17, p. 557–587.

- CHEN, Z.T. AND YAO, J.H., 1993, Paleozoic Echinoderm Fossils of Western Yunnan, China: Geological Publishing House, Beijing, 102 p.
- CHRISTENSEN, A.M., 1999, Brachiopod paleontology and paleoecology of the Lower Mississippian Lodgepole Limestone in southeastern Idaho, *in* S.S. Hughes and G.D. Thackray (eds.), Guidebook to the Geology of Eastern Idaho: Idaho Museum of Natural History, Pocatello, p. 57–67.
- CISNE, J.L. AND RABE, B.D., 1978, Coenocorrelation: gradient analysis of fossil communities and its applications in stratigraphy: Lethaia, v. 11, p. 341–364.
- COBBAN, W.A., 1945, Marine Jurassic formations of Sweetgrass Arch, Montana: American Association of Petroleum Geologists Bulletin, v. 29, p. 1262–1303.
- COHEN, K.M., FINNEY, S.C., GIVVARD, P.L., AND FAN, J.X., 2013, The ICS International Chronostratigraphic Chart: Episodes, v. 36, p. 199–204.
- CLARKE, K.R., 1993, Non-parametric multivariate analyses of changes in community structure: Australian Journal of Ecology, v. 18, p. 117–143.
- DEBOUT, J. AND DENAYER, J., 2018, Palaeoecology of the upper Tournaisian (Mississippian) crinoidal limestones from South Belgium: Geologica Belgica, v. 24, p. 111–127.
- DINEEN, A.A., FRAISER, M.L., AND ISBELL, J.L., 2013, Palaeoecology and sedimentology of Carboniferous glacial and post-glacial successions in the Paganzo and Río Blanco basins of northwestern Argentina: Geological Society of London Special Publications, v. 376, p. 109–140.
- DOTT, R.H. AND BOURGEOIS, J., 1982, Hummocky stratification: significance of its variable bedding sequences: Geological Society of America Bulletin, v. 93, p. 663–680.
- DROSER, M.L. AND BOTTJER, D.J., 1986, A semiquantitative field classification of ichnofabric: Journal of Sedimentary Research, v. 56, p. 558–559.
- DUKE, W.L., 1985, Hummocky cross-stratification, tropical hurricanes, and intense winter storms: Sedimentology, v. 32, p. 167–194.
- DUNHAM, R.J., 1962, Classification of carbonate rocks according to depositional texture, *in* W.E. Ham (ed.), Classification of Carbonate Rocks: American Association of Petroleum Geologists Memoir, v. 1, p. 108–121.
- ELIAS, R.J., ZEILSTRA, R.G., AND BAYER, T.N., 1988, Paleoenvironmental reconstruction based on horn corals, with an example from the Late Ordovician of North America: PALAIOS, v. 3, p. 22–34.
- ELRICK, M. AND READ, J.F., 1991, Cyclic ramp-to-basin carbonate deposits, Lower Mississippian, Wyoming and Montana: a combined field and computer modeling study: Journal of Sedimentary Petrology, v. 61, p. 1194–1224.
- ELRICK, M., READ, J.F., AND CORUH, C., 1991, Short-term paleoclimatic fluctuations expressed in Lower Mississippian ramp-slope deposits, southwestern Montana: Geology, v. 19, p. 799–802.
- EMBRY, A.F. AND JOHANNESSEN, E.P., 1992, T–R sequence stratigraphy, facies analysis and reservoir distribution in the uppermost Triassic–Lower Jurassic succession, western Sverdrup Basin, Arctic Canada, *in* T.O. Vorren, E. Bergsager, O.A. Dahl-Stamnes, E. Holter, B. Johansen, E. Lie, and T.B. Lund (eds.), Arctic Geology and Petroleum Potential: Norwegian Petroleum Society Special Publication, v. 2, p. 121–146.
- ERWIN, D.H., 1989, Regional paleoecology of Permian gastropod genera, Southwestern United States and the End-Permian mass extinction: PALAIOS, v. 4, p. 424–438.
- FELDMAN, H.R., BROWN, M.A., AND ARCHER, A.W., 1993, Benthic assemblages as indicators of sediment stability: evidence from grainstones of the Harrodsburg and Limestones Salem (Mississippian, Indiana), *in* B.D. Kieth and C.W. Zuppmann (eds.), Mississippian Oolites and Modern Analogs: American Association of Petroleum Geologists Studies in Geology, v. 35, p. 115–128.
- FLügel, E., 2010, Microfacies of Carbonate Rocks: Analysis, Interpretation and Application: Springer, London, 984 p.
- FOSTER, W.J., DANISE, S., SEDLACEK, A., PRICE, G.D., HIPS, K., AND TWITCHETT, R.J., 2015, Environmental controls on post-Permian recovery of benthic, tropical marine ecosystems in western Palaeotethys (Aggtelek Karst, Hungary): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 440, p. 374–394.
- FÜRSICH, F.T. AND HURST, J.M., 1974, Environmental factors determining the distribution of brachiopods: Palaeontology, v. 17, p. 879–900.
- GARRETT, P., 1977, Biological communities and their sedimentary record, in L.A. Hardie (ed.), Sedimentation on the Modern Carbonate Flats of Northwest Andros Island: Johns Hopkins University Studies in Geology, v. 22, p. 124–158.
- GUTSCHICK, R.C. AND SANDBERG, C.A., 1983, Mississippian continental margins of the conterminous United States: SEPM Special Publication, v. 33, p. 79–96.
- GUTSCHICK, R.C., SANDBERG, C.A., AND SANDO, W.J., 1980, Mississippian shelf margin and carbonate platforms from Montana to Nevada, *in* T.D. Fouch and E.R. Magathan (eds.), Paleozoic Paleogeography of the West-Central United States: Rocky Mountain Paleogeography Symposium, v. 1, p. 111–128.
- HALLEY, R.B., HARRIS, P.M., AND HINE, A.C., 1983, Bank margin environments, *in* P.A. Schoole, D.G. Bebout, and C.H. Moore (eds.), Carbonate Depositional Environments: American Association of Petroleum Geologists Memoir, v. 33, p. 463–506.
- HARRIS, P.M., 1979, Facies Anatomy and Diagenesis of a Bahamian Ooid Shoal: Sedimenta VII: Comparative Sedimentology Lab, Miami, p. 163.
- HENDY, A.J.W., 2013, Spatial and stratigraphic variation of marine paleoenvironments in the middle-upper Miocene Gatun Formation, Isthmus of Panama: PALAIOS, v. 28, p. 210– 227.
- HINE, A.C., 1977, Lily Bank, Bahamas: history of an active ooid sand shoal: Journal of Sedimentary Petrology, v. 47, p. 1554–1581.

- HOLLAND, S.M., MILLER, A.I., MEYER, D.L., AND DATTILO, B.F., 2001, The detection and importance of subtle biofacies within a single lithofacies: the Upper Ordovician Kope Formation of the Cincinnati, Ohio Region: PALAIOS, v. 16, p. 205–217.
- HOLLAND, S.M. AND PATZKOWSKY, M.E., 2004, Ecosystem structure and stability: middle Upper Ordovician of Central Kentucky, USA: PALAIOS, v. 19, p. 316–331.
- INGRAM, R.L., 1954, Terminology for thickness of stratification and parting units in sedimentary rocks: Geological Society of America Bulletin, v. 65, p. 937–938.
- JOHNSTON, D.I., HENDERSON, C.M., AND SCHMIDT, M.J., 2010, Upper Devonian to Lower Mississippian conodont biostratigraphy of uppermost Wabamun Group and Palliser Formation to lowermost Banff and Lodgepole formations, southern Alberta and southeastern British Columbia, Canada: implications for correlations and sequence stratigraphy: Bulletin of Canadian Petroleum Geology, v. 58, p. 295–341.
- KAMMER, T.W. AND AUSICH, W.I., 1987, Aerosol suspension feeding and current velocities: distributional controls for late Osagean crinoids: Paleobiology, v. 13, p. 379–395.
- KAMMER, T.W. AND AUSICH, W.I., 2006, The "Age of Crinoids": a Mississippian biodiversity spike coincident with widespread carbonate ramps: PALAIOS, v. 21, p. 238–248.
- KAMMER, T.W., BAUMILLER, T.K., AND AUSICH, W.I., 1997, Species longevity as a function of niche breadth: evidence from fossil crinoids: Geology, v. 25, p. 219–222.
- KAMMER, T.W., BAUMILLER, T.K., AND AUSICH, W.I., 1998, Evolutionary significance of differential species longevity in Osagean–Meramecian (Mississippian) crinoid clades: Paleobiology, v. 24, p. 155–176.
- KIDWELL, S.M. AND BOSENCE, D.W.J., 1991, Taphonomy and time-averaging of marine shelly faunas, in P.A. Allison and D.E.G. Briggs (eds.), Taphonomy: Releasing the Data Locked in the Fossil Record: Plenum Press, New York, p. 115–209.
- KOLDE, R., 2019, pheatmap: pretty heatmap: R package version 1.0.12, https://CRAN.Rproject.org/package=pheatmap.
- KOWALEWSKI, M., GÜRS, K., NEBELSICK, J.H., OSCHMANN, W., PILLER, W.E., AND HOFFMEISTER, A.P., 2002, Multivariate hierarchical analyses of Miocene mollusk assemblages of Europe: paleogeographic, paleoecological, and biostratigraphic implications: Geological Society of America Bulletin, v. 114, p. 239–256.
- KRUSKAL, J.B., 1964a, Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis: Psychometrika, v. 29, p. 1–27.
- KRUSKAL, J.B., 1964b, Nonmetric multidimensional scaling: a numerical method: Psychometrika, v. 29, p. 115–129.
- LAFFERTY, A.G., MILLER, A.I., AND BRETT, C.E., 1994, Comparative spatial variability in faunal composition along two Middle Devonian paleoenvironmental gradients: PALAIOS, v. 9, p. 224–236.
- LAUDON, L.R., 1967, Ontogeny of the Mississippian crinoid *Platycrinites bozemanensis* (Miller and Gurley), 1897: Journal of Paleontology, v. 41, p. 1492–1497.
- LAUDON, L.R. AND SEVERSON, J.L., 1953, New crinoid fauna, Mississippian, Lodgepole Formation, Montana: Journal of Paleontology, v. 27, p. 505–536.
- LEBOLD, J.G. AND KAMMER, T.W., 2006, Gradient analysis of faunal distributions associated with rapid transgression and low accommodation space in a Late Pennsylvanian marine embayment: biofacies of the Ames Member (Glenshaw Formation, Conemaugh Group) in the northern Appalachian Basin, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 231, p. 291–314.
- MACHEL, H.G., 2004, Concepts and models of dolomitization: a critical reappraisal, *in* C.J.R. Braithwaite, G. Rizzi, and G. Darke (eds.), The Geometry and Petrogenesis of Dolomite Hydrocarbon Reservoirs: Geological Society of London Special Publications, v. 235, p. 7–63.
- MAECHLER, M., ROUSSEEUW, W.P., STRUYF, A., HUBERT, M., AND HORNIK, K., 2019, cluster: cluster analysis basics and extensions: R package version 2.1.0, https://CRAN.R-project. org/package=cluster
- MARTIN, K.D., 2004, A re-evaluation of the relationship between trace fossils and dysoxia, in D. McIlroy (ed.), The Application Ichnology to Palaeoenvironmetnal and Stratigraphic Analysis: Geological Society of London Special Publications, v. 228, p. 141–156.
- MAUGHAN, E.K., 1983, Tectonic setting of the Rocky Mountain region during the late Paleozoic and the early Mesozoic, *in* J.W. Babcock (ed.), Proceedings of Symposium on the Genesis of Rocky Mountain Ore Deposits: Changes with Time and Tectonics: Denver Regional Exploration Geologists Society, Denver, p. 39–50.
- MAYNARD, J.B., 1982, Extension of Berner's "New geochemical classification of sedimentary environments" to ancient sediments: Journal of Sedimentary Petrology, v. 52, p. 1325–1331.
- McCUNE, B. AND GRACE, J.B., 2002, Analysis of Ecological Communities: MjM Software Design, Gleneden Beach, Oregon, 300 p.
- McKerrow, W.S. AND Scotese, C.R., 1990, Revised world maps and introduction, *in* W.S. McKerrow and C.R. Scotese (eds.), Paleozoic Paleogeography and Biogeography: Geological Society Memoir, v. 12, p. 1–24.
- MCMULLEN, S.K., HOLLAND, S.M., AND O'KEEFE, F.R., 2014, The occurrence of vertebrate and invertebrate fossils in a sequence stratigraphic context: the Jurassic Sundance Formation, Bighorn Basin, Wyoming, USA: PALAIOS, v. 29, p. 227–294.
- MEISTER, P., MCKENZIE, J.A., BERNASCONI, S.M, AND BRACK, P., 2013, Dolomite formation in the shallow seas of the Alpine Triassic: Sedimentology, v. 60, p. 270–291.
- MELIM, L.A. AND SCHOLLE, P.A., 2002, Dolomitization of the Capitan Formation forereef facies (Permian, west Texas and New Mexico): seepage reflux revisited: Sedimentology, v. 49, p. 1207–1227.

- MONROE, W.H., 1970, A glossary of karst terminology: U.S. Geological Survey Water-Supply Paper 1899-K, p. 1–26.
- MOORE, G.T., 1973, Lodgepole Limestone facies in southwestern Montana: American Association of Petroleum Geologists Bulletin, v. 57, p. 1703–1713.
- MUDGE, M.R., SANDO, W.J., AND DUTRO, J.T., 1962, Mississippian rocks of Sun River Canyon area, Sawtooth Range, Montana: American Association of Petroleum Geologists Bulletin, v. 46, p. 2003–2018.
- MUNSELL COLOR, 1976, Munsell Book of Color: Matte Finish Collection: Kollmorgen Corporation, Baltimore, Maryland, 40 p.
- NOVACK-GOTTSHALL, P.M. AND MILLER, A.I., 2003, Comparative taxonomic richness and abundance of Late Ordovician gastropods and bivalves in mollusc-rich strata of the Cincinnati Arch: PALAIOS, v. 18, p. 559–571.
- OKSANEN. J., 2019, metaMDS, in J. Oksanen, F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, and H. Wagner (eds.), vegan: Community Ecology Package: R package version 2.5-5, https://CRAN.R-project.org/package=vegan.
- OLSZEWSKI, T.D. AND PATZKOWSKY, M.E., 2001, Measuring recurrence of marine biotic gradients: a case study from the Pennsylvanian–Permian Midcontinent: PALAIOS, v. 16, p. 444–460.
- PATZKOWSKY, M.E., 1995, Gradient analysis of Middle Ordovician brachiopod biofacies: biostratigraphic, biogeographic, and macroevolutionary implications: PALAIOS, v. 10, p. 154–179.
- PATZKOWSKY, M.E. AND HOLLAND, S.M., 2012, Stratigraphic Paleobiology: Understanding the Distribution of Fossil Taxa in Time and Space: The University of Chicago Press, Chicago, 255 p.
- PERERA, S.N. AND STIGALL, A.L., 2018, Identifying hierarchical spatial patterns within paleocommunities: an example from the Upper Pennsylvanian Ames Limestone of the Appalachian Basin: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 506, p. 1–11.
- PIPER, D.Z. AND CALVERT, S.E., 2009, A marine biogeochemical perspective on black shale deposition: Earth-Science Reviews, v. 95, p. 63–96.
- POOLE, F.G. AND SANDBERG, C.A., 1977, Mississippian paleogeography and tectonics of the western United States, *in* J.H. Stewart, C.H. Stevens, and A.E. Fritsche (eds.), Paleozoic Paleogeography of the Western United States: SEPM Pacific Coast Paleogeography Symposium 1, SEPM, Tulsa, p. 67–86.
- R CORE TEAM, 2019, R: A Language and Environment for Statistical Computing: R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org.
- READ, J.F., 1985, Carbonate platform facies models: American Association of Petroleum Geologists Bulletin, v. 69, p. 1–21.
- REDMAN, C.M., LEIGHTON, L.R., SCHELLENBERG, S.A., GALE, C.N., NIELSEN, J.L., DRESSLER, D.L., AND KLINGER, M.K., 2007, Influence of spatiotemporal scale on the interpretation of paleocommunity structure: lateral variation in the Imperial Formation of California: PALAIOS, v. 22, p. 630–641.
- REID, R.P. AND MACINTYRE, I.G., 1998, Carbonate recrystallization in shallow marine environments: a widespread diagenetic process forming micritized grains: Journal of Sedimentary Research, v. 68, p. 928–946.
- REID, R.P., MACINTYRE, I.G., AND POST, J.E., 1992, Micritized skeletal grains in northern Belize lagoon: a major source of Mg-calcite mud: Journal of Sedimentary Petrology, v. 62, p. 145–156.
- REID, S.K. AND DOROBEK, S.L., 1993, Sequence stratigraphy and evolution of a progradational, foreland carbonate ramp, Lower Mississispipan Mission Canyon Formation and stratigraphic equivalents, Montana and Idaho, *in* R.G. Loucks and J.F. Sarg (eds.), Carbonate Sequence Stratigraphy: Recent Developments and Applications: American Association of Petroleum Geologists Memoir, v. 57, p. 327–352.
- RODRIGUEZ, J. AND GUTSCHICK, R.C., 1968, *Productina*, *Cyrtina*, and *Dielasma* (Brachiopoda) from the Lodgepole Limestone (Mississippian) of southwestern Montana: Journal of Paleontology, v. 42, p. 1027–1032.
- RODRIGUEZ, J. AND GUTSCHICK, R.C., 1969, Silicified brachiopods from the lower Lodgepole Limestone (Kinderhookian), southwestern Montana: Journal of Paleontology, v. 43, p. 952–960.
- RUDWICK, M.J.S., 1970, Living and Fossil Brachiopods: Hutchinson and Company, London, 199 p.
- SANDO, W.J., 1960, Corals from well cores of Madison Group, Williston Basin: United States Geological Survey Bulletin, v. 1071-F, p. 157–190.
- SANDO, W.J., 1976, Mississippian history of the northern Rocky Mountains region: Journal of Research, U.S. Geological Survey, v. 4, p. 317–338.
- SANDO, W.J., 1980, The paleoecology of Mississippian corals in the western conterminous United States: Acta Palaeontologica Polonica, v. 25, p. 619–637.
- SANDO, W.J., 1985, Revised Mississippian time scale, western interior region, conterminous United States: U.S. Geological Survey Bulletin 1605A, p. A15–A26.
- SAVRDA, C.E., 2007, Trace fossils and marine benthic oxygenation, *in* W. Miller (ed.), Trace Fossils: Concepts, Problems, Prospects: Elsevier, Amsterdam, p. 149–158.
- SAVRDA, C.E. AND BOTTJER, D.J., 1986, Trace fossil model for reconstruction of palaeooxygenation in bottom waters: Geology, v. 14, p. 3–6.
- SAVRDA, C.E., BOTTJER, D.J., AND GORSLINE, D.S., 1984, Development of a comprehensive oxygen-deficient marine biofacies model: evidence from Santa Monica, San Pedro, and Santa Barbara Basins, California Continental Borderland: American Association of Petroleum Geologists Bulletin, v. 68, p. 1179–1192.

TAIT, R.V. AND DIPPER, F.A., 1998, Elements of Marine Ecology: Butterwork-Heinemann, Oxford, 462 p.

- SCARPONI, D., HUNTLEY, J.W., CAPRARO, L., AND RAFFI, S., 2014, Stratigraphic paleoecology of the Valle di Manche section (Crotone Basin, Italy): a candidate GSSP of the Middle Pleistocene: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 402, p. 30–43.
- SCARPONI, D. AND KOWALEWSKI, M., 2004, Stratigraphic paleoecology: bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy: Geology, v. 32, p. 989–992.
- SCRUTTON, C.T., 1998, The Palaeozoic corals, II: structure, variation and palaeoecology: Proceedings of the Yorkshire Geological Society, v. 52, p. 1–57.
- SHAW, A.B., 1962, Rhynchonellid brachiopods and a *Torynifer* from the Madison Group (Mississippian): Journal of Paleontology, v. 36, p. 630–637.
- SHINN, E.A., 1968, Burrowing in recent lime sediments of Florida and the Bahamas: Journal of Paleontology, v. 42, p. 879–894.
- SHOURD, M.L. AND LEVIN, H.L., 1976, Chondrites in the Upper Plattin Subgroup (Middle Ordovician) of eastern Missouri: Journal of Paleontology, v. 50, p. 260–268.
- SMITH, L.B., EBERLI, G.P., AND SONNENFELD, M., 2004, Sequence-stratigraphic and paleogeographic distribution of reservoir-quality dolomite, Madison Formation, Wyoming and Montana, *in* G.M. Grammar, P.M. Harris, and G.P. Eberli (eds.), Integration of Outcrop and Modern Analogs in Reservoir Modeling: American Association of Petroleum Geologists Memoir, v. 80, p. 67–92.
- SMITH, L.B. AND READ, J.F., 1999, Application of high-resolution sequence stratigraphy to tidally influenced Upper Mississippian carbonates, Illinois Basin, *in* P.M. Harris, A.H. Saller, and J.A. Simo (eds.), Advances in Carbonate Sequence Stratigraphy: Application to Reservoirs, Outcrops, and Models: SEPM Special Publication, v. 63, p. 107–126.
- SMITH, L.B. AND READ, J.F., 2001, Discrimination of local and global effects on Upper Mississippian stratigraphy, Illinois Basin, U.S.A.: Journal of Sedimentary Research, v. 71, p. 985–1002.
- SONNENFELD, M.D., 1996, Sequence evolution and hierarchy within the lower Mississippian Madison Limestone of Wyoming, *in* M.W. Longman and M.D. Sonnenfeld (eds.), Paleozoic Systems of the Rocky Mountain Region: Rocky Mountain Section SEPM, p. 165–192.
- TAYLOR, A., GOLDRING, R., AND GOWLAND, S., 2003, Analysis and application of ichnofabrics: Earth Science Reviews, v. 60, p. 227–259.
- TER BRAKK, C.J.F., 1986, Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis: Ecology, v. 67, p. 1167–1179.
- TOMAŠOVÝCH, A., 2006, Brachiopod and bivalve ecology in the Late Triassic (Alps, Austria): onshore-offshore replacements caused by variations in sediment and nutrient supply: PALAIOS, v. 24, p. 344–368.

- TUCKER, M.E. AND WRIGHT, P., 1990, Carbonate Sedimentology: Blackwell Scientific Publications, Oxford, 482 p.
- VAN WAGONER, J.C., POSAMENTIER, H.W., MITCHUM, R.M., VAIL, P.R., SARG, J.F., LOUTIT, T.S., AND HARDENBOL, J., 1988, An overview of sequence stratigraphy and key definitions, *in* C.K. Wilgus, B.S. Hastings, C.G. St. C. Kendall, H.W. Posamentier, C.A. Ross, J.C. Van Wagoner (eds.), Sea Level Changes—An Integrated Approach: SEPM Special Publications, v. 42, p. 39–45.
- WANLESS, H.R., BURTON, E.A., AND DRAVIS, J., 1981, Hydrodynamics of carbonate fecal pellets: Journal of Sedimentary Petrology, v. 51, p. 27–36.
- WANLESS, H.R. AND TEDESCO, L.P., 1993, Comparison of oolitic sand bodies generated by tidal vs. wind-wave agitation, *in* B.D. Kieth and C.W. Zuppmann (eds.), Mississippian Oolites and Modern Analogs: American Association of Petroleum Geologists Studies in Geology, v. 35, p. 199–225.
- WATERS, D.L. AND SANDO, W.J., 1987, Corals from the Madison Group, Williston Basin, North Dakota, in C.G. Carlson and J.E. Christopher (eds.), Fifth International Williston Basin Symposium: Saskatchewan Geological Society Special Publication, v. 9, p. 83–97.
- WATERS, J.A. AND SEVASTOPULO, G.D., 1984, The stratigraphical distribution and palaeoecology of Irish Lower Carboniferous blastoids: Irish Journal of Earth Sciences, v. 6, p. 137–154.
- WEBBER, A.J., 2002, High-resolution faunal gradient analysis and an assessment of the causes of meter-scale cyclicity in the type Cincinnatian Series (Upper Ordovician): PALAIOS, v. 17, p. 545–555.
- WEBBER, A.J., 2005, The effects of spatial patchiness on the stratigraphic signal of biotic composition (type Cincinnatian Series; Upper Ordovician): PALAIOS, v. 20, p. 37–50.
- WEBSTER, G.D., MAPLES, C.G., MAWSON, R., AND DASTANPOUR, M., 2003, A cladiddominated early Mississippian crinoid and conodont fauna from Kerman province, Iran and revision of the glossocrinids and rhenocrinids: Journal of Paleontology, v. 77, p. 1– 36.
- WETZEL, A. AND UCHMAN, A., 1998, Deep-sea benthic food content recorded by ichnofabrics: a conceptual model based on observations from Paleogene flysch, Carpathians, Poland: PALAIOS, v. 13, p. 533–546.
- WHITTAKER, R.H., 1956, Vegetation of the Great Smoky Mountains: Ecological Monographs, v. 26, p. 1–80.
- ZUSCHIN, M., HARZHAUSER, M., HENGST, B., MANDIC, O., AND ROETZEL, R., 2014, Long-term ecosystem stability in an Early Miocene estuary: Geology, v. 42, p. 7–10.

Received 23 July 2020; accepted 24 January 2021.