Ecological Signature of Lower Triassic Shell Beds of the Western United States

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The end-Permian mass extinction was the largest Phanerozoic biotic crisis that resulted in significant and permanent ecological change. In order to examine ecological aspects of the recovery, shell beds deposited in environments ranging from nearshore to storm wave base were examined from three stratigraphic intervals in the Lower Triassic of the western U.S. Shell beds of the first interval, the Griesbachian Dinwoody Formation, are low-diversity, monospecific beds of Claraia *and* Promyalina*, commonly with the inarticulate brachiopod* Lingula*. Data from the Nammalian Sinbad Limestone (Moenkopi Formation) provide a small window into the second time interval, in which common low-diversity (bivalves and microgastropods) shell beds occur. Within the third interval, represented by the Spathian Virgin Limestone (Moenkopi Formation) and Thaynes Formation, the bivalves* Promyalina *and* Permophorus *are found in both monospecific and polytaxic beds. Crinoids are also commonly found as encrinites and as significant contributors to the matrix of these beds. Shell beds range in thickness from pavements to 10s of centimeters and show variable internal complexity. The persistence of monospecific shell beds throughout these three intervals is significant as support for long-term stress during the recovery interval that is not apparent from sedimentological data alone. Although these Early Triassic beds primarily are comprised of members of the Modern Evolutionary Fauna, they are more similar to beds from the Paleozoic in thickness and taphonomic characteristics.*

INTRODUCTION

Shell beds, or dense accumulations of fossils, are formed through a combination of mechanical and biological processes. While the sedimentological and stratigraphic significance of fossil concentrations is well recognized (e.g., Kidwell, 1986, 1991; Kidwell and Holland, 1991; Fürsich and Oschmann, 1993), fossil concentrations have not commonly been used for ecological studies because of obvious issues of temporal and spatial averaging. Recent work has suggested that shell beds accurately record broad-scale ecological changes and provide useful proxies for changes in patterns of dominance and abundance through geologic time (Li and Droser, 1999; Boyer and Droser, 2003).

The end-Permian mass extinction was the largest biotic crisis of the Phanerozoic, during which possibly as many as 96% of species became extinct (Raup, 1979; Hallam and Wignall, 1997). A variety of mechanisms have been implicated in the end-Permian mass extinction, including marine anoxia, eruption of the Siberian traps, and hypercapnia (CO_2 poisoning), and debate continues on whether the crisis represents one event or two in close succession (e.g., Hallam and Wignall, 1997). Whatever the cause, end-Permian environmental conditions wreaked such havoc on Earth's biota that the succeeding Early Triassic appears to represent an unusually long recovery interval from a mass extinction.

This protracted recovery through the Early Triassic records a massive ecological turnover that resulted in a major shift in dominance in marine soft substrate communities as well as a major restructuring of carbonate buildups (Raup, 1979; Erwin, 1993, 1994; Bottjer, et al., 2001). Communities at this time were simple, of low taxonomic diversity, and cosmopolitan (Hallam, 1991; Schubert and Bottjer, 1995). This study examines Lower Triassic shell beds through the recovery interval in the Basin and Range and Rocky Mountain Regions and illustrates the utility of fossil concentrations as a tool to examine the dynamics of marine communities.

STRATIGRAPHIC AND GEOLOGICAL SETTING

Lower Triassic marine strata in the western United States represent broad deposition of shallow-water carbonate and mixed carbonate-siliciclastic deposits that are well preserved and exposed in the Great Basin and Rocky Mountain provinces (Fig. 1). Three major transgressive events resulted in the deposition of rock representing three successive major seaways (Schubert and Bottjer, 1995). These seaways represent three distinct time slices and allow for a time-transgressive look at the signature of shell beds through the recovery interval (Fig. 2).

The first transgressive event, which is Griesbachian in age, resulted in mixed carbonate-siliciclastic deposition of the Dinwoody Formation, and is restricted to the northern part of the study area, including Montana, Wyoming, Idaho, and north-central Utah (Paull et al., 1989; Schubert

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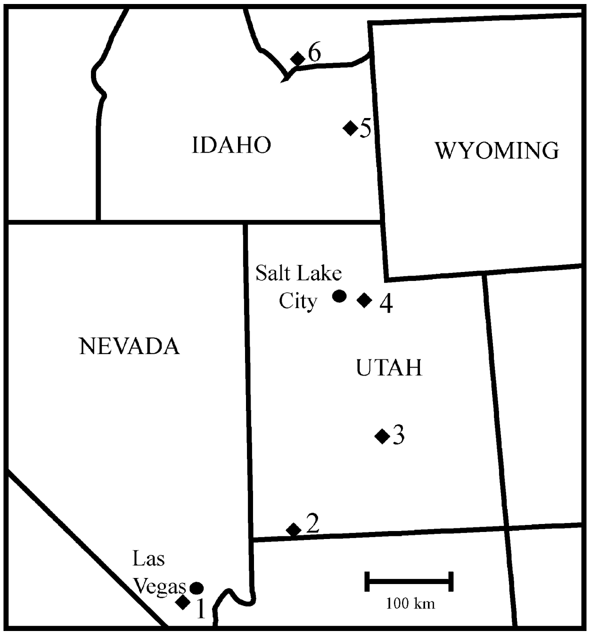

FIGURE 1—Location of Lower Triassic field localities (after Schubert and Bottjer, 1995). (1) Lost Cabin Springs (Virgin limestone); (2) Hurricane (Virgin limestone); (3) San Rafael Swell (Sinbad limestone); (4) Cascade Springs (Thaynes Formation); (5) Fall Creek (Thaynes Formation); (6) Hidden Pasture (Dinwoody Formation).

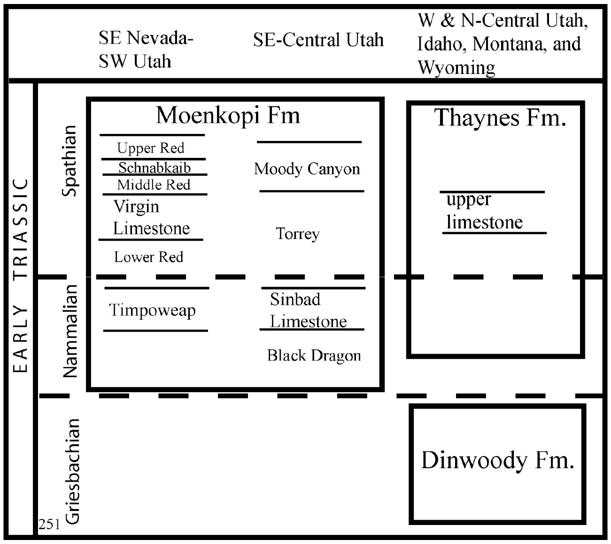

FIGURE 2—Stratigraphy of western U.S. Lower Triassic (after Schubert and Bottjer, 1995). The Dinwoody Formation, Thaynes Formation, and the Virgin and Sinbad Limestone members of the Moenkopi Formation were examined in this study.

and Bottjer, 1995; Rodland and Bottjer, 2001). The second transgression, Nammalian in age, is represented by massive carbonate deposition and the occurrence of the ammonoid *Meekoceras* (Kummel, 1954). The Moenkopi Formation represents deposition through both the second (Nammalian) and third (Spathian) transgressions, but is given different nomenclature in southeastern Utah than in southwestern Utah and southeastern Nevada (Dean, 1981; Fig. 2). The second transgression was more extensive than the first, and is well represented in southeastern and central Utah by the Sinbad Limestone Member of the Moenkopi Formation (Dean, 1981). The third (Spathian) transgressive event is represented in this study by the Virgin Limestone Member of the Moenkopi Formation in the southwestern part of the study area, and the upper Thaynes Formation in the northern and northeastern portion of the study area (Kummel, 1954; Reif and Slatt, 1979). This third transgressive event resulted in the most extensive shallow seaway in the western U.S. during the Early Triassic (Carr and Paull, 1983).

METHODS

Detailed stratigraphic sections were recorded at six localities (Lost Cabin Springs, Hurricane, San Rafael Swell, Cascade Springs, Fall Creek, Hidden Pasture) representing all three time slices (Fig. 1). Localities with characteristic depositional environments and preservation were selected based on previous studies and reconnaissance field work to avoid a taphonomic bias (e.g., Schubert and Bottjer, 1995; Rodland and Bottjer, 2001). Shell beds were described in the field and in the laboratory using methods outlined by Kidwell et al. (1986), Kidwell (1991), and Kidwell and Holland (1991). In the field, the thickness, lateral extent, contact surfaces, and geometries of fossil concentrations were recorded along with taxonomic and taphonomic data from each shell bed. Particular attention was given to the taphonomic conditions of bioclasts and internal fabrics of shell beds seen in cross-section both in the field and in the laboratory. Emphasis was placed on the taphonomic characteristics of these shell beds because they are essential for determining the extent to which bioclasts in these shell beds were transported from their original life position, and, therefore, how closely these deposits represent original communities. Specifically, the degree of fragmentation, sorting, presence of graded beds, density or packing of shell material (densely, loosely, dispersed), orientation and convexity of individual shells, and the matrix composition were recorded from each fossil concentration. The presence of articulated specimens also was noted from field and laboratory work because it indicates minimal transport. In the field, shell beds were traced laterally to determine the spatial fidelity of the taphonomic and taxonomic signatures in these deposits.

Multiple samples of each bed type, based on taxonomic and taphonomic characteristics, were collected in the field, but because of the large number of individual beds, each bed was not sampled in detail. Collected samples were cut into slabs and polished in the laboratory. Acetate peels were made for closer examination of the internal fabric of the shell beds. Length measurements of one species of *Permophorus* or *Promyalina* from well-exposed bedding planes were used to test for sorting and, ultimately, degree of transport. Concentrations of crinoid debris pose a problem for comparative studies of fossil concentrations because commonly, bioclasts are less than 2 mm in size, and are therefore traditionally excluded from such studies (Kidwell, 1986; Kidwell and Brenchley, 1994; Li and Droser, 1999). As a result, crinoid debris present as a contributor to the matrix of a shell bed typically is not recorded. Although the number of individual crinoids cannot be calculated from the abundance of small fragments preserved

TABLE 1—Descriptions of Lower Triassic shell beds by stratigraphic unit.

	Dinwoody	Sinbad	Virgin/Thaynes
Environment	Inner shelf	Nearshore	Inner shelf
Packing	Loosely–loosely/densely	Densely	Loosely to densely
Internal stratigraphy	Simple	Simple	Simple
Fragmentation	Low	High	Low–high
Common Taxa	*Lingula, Claraia*	Microgastropods, bivalves	Bivalves, echinoderms
Diversity	Monospecific	Monospecific–polytaxic	Monospecific–polytaxic

in shell beds in this study, encrinites are reported as bioclastic accumulations and the relative abundance of these types of shell beds is recorded (Table 1).

Dominance and evenness calculations typically are not calculated for fossil concentrations because these deposits likely represent averaged communities. However, these statistics are used for this study in order to compare the ecological signature of shell beds from each time slice. The use of these measures in no way implies that these concentrations necessarily represent ecological communities. However, beds were selected for these calculations that showed the least taphonomic bias (e.g., sorting). Evenness was calculated using the Shannon index (Shannon, 1948) and dominance was quantified using Simpson's lambda (Simpson, 1949).

Shell beds from these localities are divided into three types of beds by taxonomic composition. Monospecific beds are comprised of 95% one species (see Li and Droser, 1999). Monotaxic beds are comprised of 95% of one taxonomic group, but more than one species. For example, the microgastropod beds in this study are classified as monotaxic because they are comprised of 95% or more gastropods that are less than 1 cm in length (Fraiser and Bottjer, 2004), but have a specific diversity ranging from 7 to 26 species. In this study, the classification of a polytaxic bed is used to represent fossil concentrations that are comprised of two or more higher (ordinal level or above) taxonomic groups, such as crinoids and gastropods.

RESULTS

Descriptions of Shell Beds

Shell beds are common in all three intervals through the Lower Triassic. These fossil concentrations are interpreted mostly as event beds deposited between fair-weather and maximum storm wave base. Taphonomy and taxonomic composition, including dominant bioclast contributors and relative diversities of shell beds, are discussed for each of three intervals below (Tables 1, 2).

Griesbachian—Dinwoody Formation: The Dinwoody Formation represents deposition in an inner-shelf subtidal environment (Paull et al., 1989; Schubert and Bottjer, 1995). It is comprised primarily of mudstone and siltstone with numerous limestone interbeds that increase in frequency up-section, and are most commonly bioclast supported (Schubert and Bottjer, 1995; Rodland and Bottjer, 2001; Fig. 3).

Shell beds are abundant and variable through the Dinwoody Formation. They range from thin pavements to beds 10 cm thick that represent single events or amalgamated packages of fossil concentrations. Shell beds are laterally persistent at the outcrop scale. Bioclasts within these beds are loosely to densely packed, and demonstrate a simple internal stratigraphy. Bivalve shells are generally disarticulated, but are not extensively fragmented or abraded. Although some individual beds demonstrate preferred convexity of shells (convex up), this is not consistent through the entire formation. Bioclasts within these shell beds are oriented concordant to oblique to the bedding plane. Shells are not well sorted by size, which, coupled with the lack of fragmentation and preferred convexity of shells, suggests limited transport within these shell beds.

Shell beds in the Dinwoody Formation are consistently of low taxonomic diversity (Table 2). Shell beds are dominantly monospecific, composed almost exclusively of the classic Early Triassic disaster taxa *Lingula* and *Claraia* (Schubert and Bottjer, 1995; Rodland and Bottjer, 2001), as well as the bivalve *Promyalina* (Fig. 4A). Rare polytaxic

TABLE 2—Relative abundances (normalized to 100) of representative shell beds from several localities from each interval D = Dinwoody, S = Sinbad, V = Virgin Limestone, T = Thaynes Formation). Other bivalves include the less common *Bakevellia, Neoschizodus,* and trigonacean bivalves.

	D1	D2	D3	S1	S2	S3	S4
Promyalina	3.2	2.4	100	2.1			
Permophorus				6.2	0.5	54.9	62.2
Leptochondria				88.7	98.6	10.6	27
Claraia		92.8					
Unionites	1.6				0.5	0.2	
Other bivalves						3.4	5.8
Lingula	95.2	4.8					
Microgastropod				3.1	0.5	31	5
n =	63	42	61	97	221	649	241
Shannon Index	0.222	0.303	0	0.466	0.087	1.055	0.126
Simpson Index	0.092	0.135	0	0.209	0.027	0.591	0.053

beds are commonly comprised of only *Lingula* and *Promyalina*. *Claraia* occurs in abundant, monospecific pavements towards the top of this formation. These pavements are so numerous and closely packed that they form a distinct biofabric (Fig. 4B), which gives the appearance of bedding, but is actually stacking of abundant pavements of *Claraia*.

The common packstone shellbeds of the Dinwoody Formation are interpreted to be event deposits. Although clearly not preserved *in situ,* the taphonomic condition of the shells (little fragmentation and sorting) suggests minimal transport. Thus, these deposits represent local or neighborhood communities, defined as assemblages made up of taxa that were not transported significantly and originated in close proximity to the environment of deposition. The taxonomic composition of these shell beds suggests low diversity and simple community structures through this interval.

Nammalian—Sinbad Limestone Member of the Moenkopi Formation: The Sinbad Limestone Member represents deposition in environments ranging from subtidal to supratidal (Dean, 1981). Six depositional lithofacies are recognized in this formation and mollusc-dominated shell beds commonly comprise packstone and wackestone lithologies (Fraiser and Bottjer, 2004). Shell beds in the Sinbad are most commonly densely packed, polytaxic, cross-bedded beds of comminuted shell material. Fossil concentrations range from several centimeters to nearly a meter in thickness and are laterally extensive for at least several meters. Nearly all of the fossil concentrations are densely packed and simple, and nearly homogenous internal fabrics are common. Some shell beds have distinct internal surfaces and others preserve cross-stratification. Shells are oriented concordant to perpendicular to the bedding plane, although shell fragments are commonly too small to demonstrate any type of orientation. Bioclasts are commonly heavily abraded, fragmented, disarticulated, and commonly well sorted, suggesting extensive transport or reworking of bioclasts in a high-energy environment.

Shell beds in the Sinbad Limestone are more variable than in the older Dinwoody Formation (Table 2). In this interval, shell beds typically are comprised of several species of bivalves and many species of microgastropods (Table 2), and may include scaphopods as well as uncommon *Lingula* and echinoderm fragments (Fraiser and Bottjer, 2004). Monospecific *Leptochondria* shell beds are common with fossils vertically nested (Fig. 4C). Densely packed monotaxic concentrations of microgastropods are also very common throughout this formation (Fraiser and Bottjer, 2004; Fig. 4D). Polytaxic beds including various bivalves, microgastropods, and other comminuted shell debris additionally occur in this formation.

The sedimentary structures, internal fabric, and highly fragmented and sorted nature of the bioclasts indicate that the fossil concentrations of the Sinbad limestone likely were deposited during storm events that resulted in extensive wave reworking and possible transport of shells. In this interval, polytaxic concentrations are more common than in the Dinwoody Formation. Despite this increase in the number of taxonomic groups represented in shell beds in this interval, monospecific and monotaxic beds are common. Although shell beds in the Sinbad limestone were deposited in significantly shallower water settings than those of the other two time intervals, the data from this interval are valuable in assessing the overall trend through the Early Triassic.

Spathian—Virgin Limestone Member of the Moenkopi Formation and the Thaynes Formation: The Virgin limestone is the middle limestone member of the Moenkopi Formation and represents deposition in marginal to subtidal environments (Rief and Slatt, 1979). The correlative upper limestone of the Thaynes Formation similarly represents deposition in an inner-shelf environment (Carr and Paull, 1983). Shell beds are common and expressed as resistant limestone ledges in both of these formations (Fig. 3). Shell beds from the Virgin limestone and the Thaynes Formation are examined together, and represent the third time slice in this study.

In these units, individual shell beds are commonly less than 10 cm in thickness, with amalgamated packages rarely more than 1 m in thickness. Fossil concentrations are laterally extensive over 10s of meters. Shell beds range from loosely to densely packed and most commonly have simple internal fabrics. Complex internal fabric is relatively rare and represents several distinct amalgamated events. Shells are commonly oriented concordant to oblique to the bedding plane and rarely demonstrate preferred convexity (convex up). Individual shells are typically unabraded, unfragmented, and uncommonly articulated, but high fragmentation does occur. The frequency of articulation ranges from one articulated specimen to close to 20% of the specimens articulated within a shell bed. Only one fossil concentration examined was clearly graded.

TABLE 2—Continued.

S5	V1	V2	V3	V4	V5	V6	T1	T2
		33.6	23.5	100	23.3	31.7	0.6	63
	83.7	45.1	65.7		66.7	61.7	81.6	
								15.1
							1.4	
							16.5	21.9
100	16.3	21.3	10.8		10.0	6.7		
73	43	122	213	74	30	60	515	73
0	0.936	1.209	1.185	0	1.166	1.049	0.552	0.909
0	0.57	0.674	0.641	0	0.63	0.581	0.307	0.532

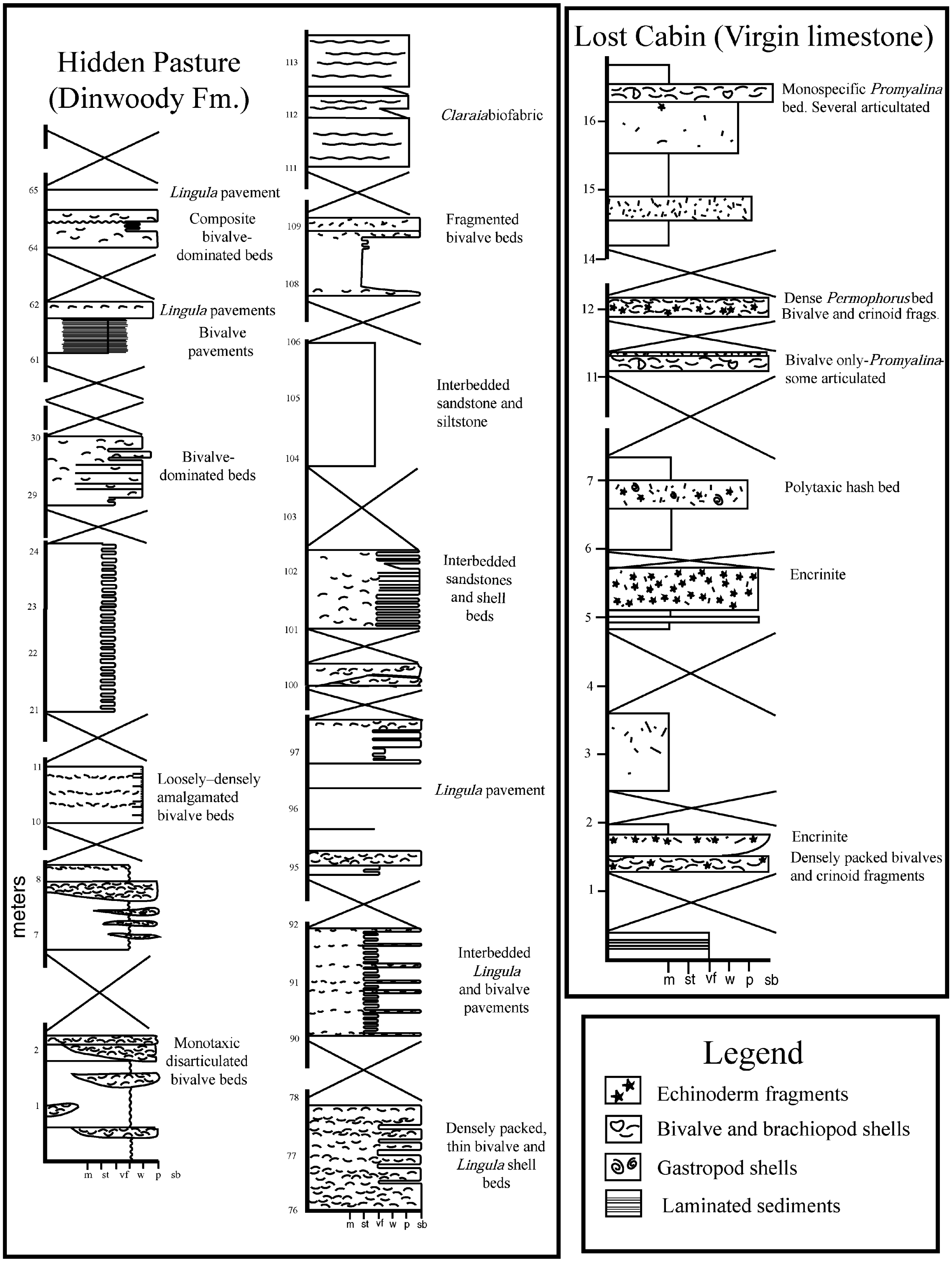

FIGURE 3—Stratigraphic sections of the Dinwoody Formation at the Hidden Pasture locality and the Virgin limestone from the Lost Cabin locality. Notice the increased variety of shell beds in the Virgin Formation (Abbreviations: m = mudstone, st = siltstone, vf = very fine sandstone, w = wackestone, p = packstone, sb = shell bed).

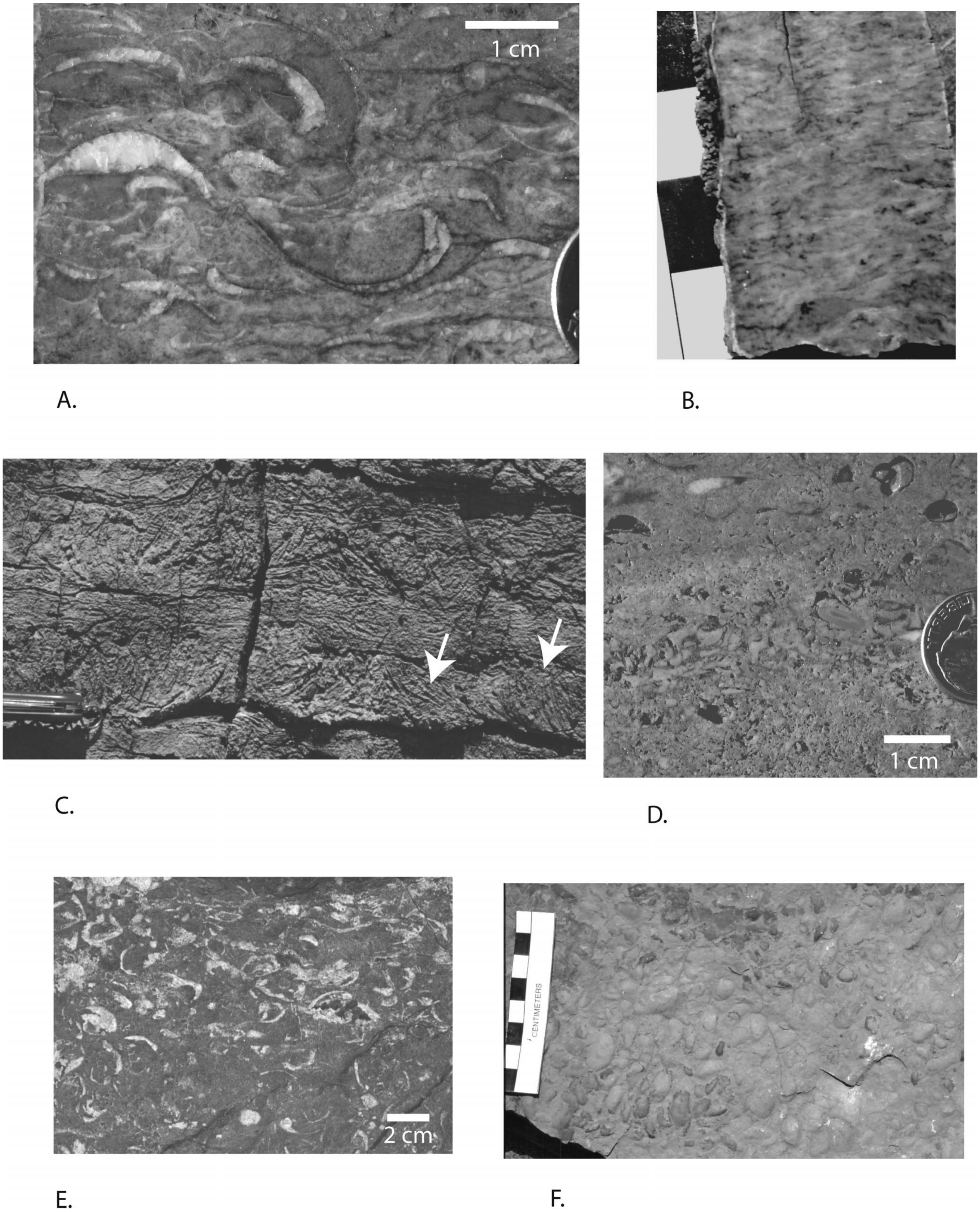

FIGURE 4—(A) Polished cross-section of monospecific *Promyalina* shell bed from the Dinwoody Formation. (B) Polished cross-section of *Claraia* biosedimentation showing close packing of abundant *Claraia* in pavement from the upper Dinwoody (scale in 1-cm increments). (C) Monospecific *Leptochondria* bed seen in cross-section from outcrop of Sinbad Limestone. Pocket knife ~1 cm thick. Arrows indicate vertically nested shells. (D) Polished cross-section of monotaxic microgastropod bed from the Sinbad limestone. (E) Polytaxic bivalve-dominated shell bed in outcrop of Thaynes Formation. (F) Bedding plane view of monospecific *Permophorus* bed from the Virgin Limestone at Hurricane.

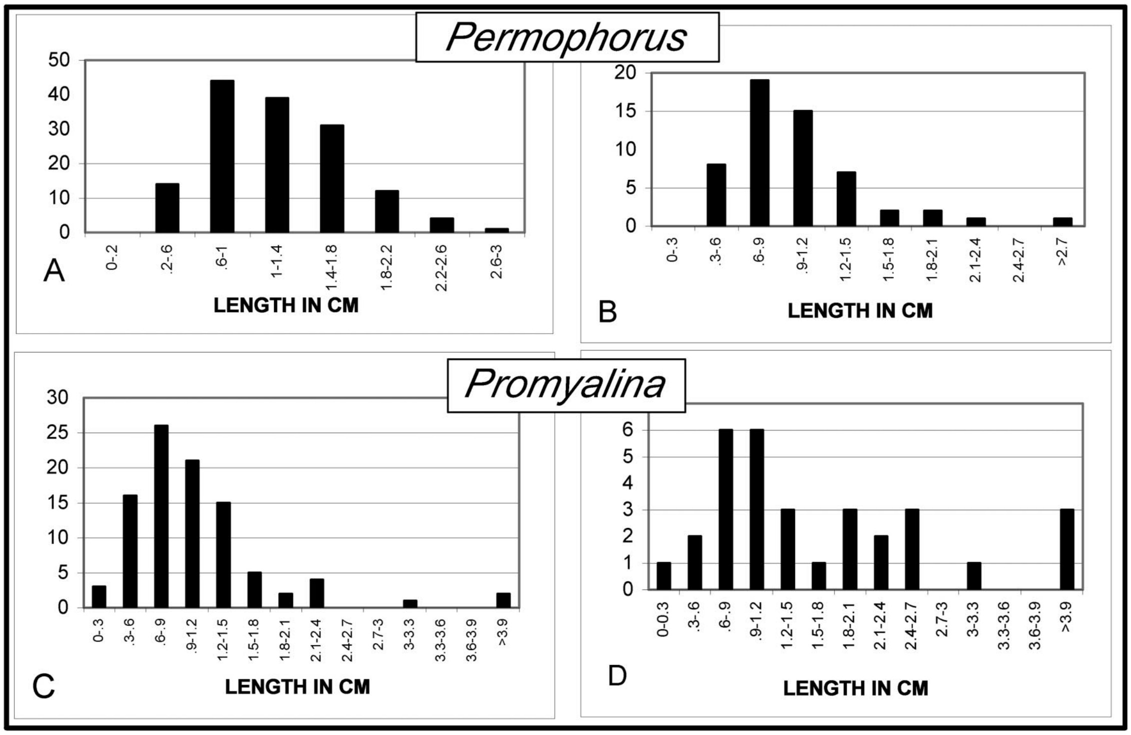

FIGURE 5—Representative size-frequency diagrams recording the length of single species of *Permophorus* and *Promyalina* from bedding-plane surfaces of shell beds from the Virgin limestone at two localities (Hurricane, Lost Cabin). Skewed distribution is consistent with a fossil population. A: n=145, B: n = 55, C: n = 95, and D: n = 31.

The amount of sorting in these concentrations was variable. Specimen lengths of single species of *Promyalina* and *Permophorus* from bedding planes showed a right-skewed distribution consistent with a fossil population (Fig. 5). This, coupled with the presence of articulated specimens and limited fragmentation of shells, suggests limited transport in some of the shell beds within these formations. Bivalves, as in the previous time slices, continue to be the most common bioclasts present in shell beds because they are the most abundant bioclast in greater than 60 % of all of the shell beds through the Spathian transgressive event (Table 2). The most abundant bivalves in this third time slice, *Promyalina* and *Permophorus*, commonly are found in both monospecific and polytaxic concentrations (Fig. 4E and 4F). Crinoid ossicles and echinoid spines first appear in this interval, and are commonly found concentrated in monospecific shell beds, as well as mixed with other taxa (Moffat and Bottjer, 1999). Echinoderm fragments are also common in the matrix of fossil concentrations. Polytaxic concentrations, ranging from two to 10s of species, with large unabraded shells first occur in this interval. Microgastropods also contribute to fossil concentrations.

Taphonomic data from shell beds of the Thaynes Formation and the Virgin limestone suggest that bioclasts are not extensively transported or reworked and represent local or neighborhood communities. Shell beds within this interval are interpreted to represent storm events operating in a subtidal environment. There is an increase in the number of different bioclast producers, including crinoids, echinoids, several rhynchonelliform brachiopods, and several new genera of bivalves, resulting in an increase in the variety of shell beds within this interval. However, low-diversity beds, including monospecific concentrations, are still common.

DISCUSSION

Lower Triassic shell beds exhibit several important characteristics. Shell beds are common throughout these intervals even though the Early Triassic is a time of protracted recovery (Bottjer, et al., 1995). Dense concentrations of bioclasts are a major part of the stratigraphic record at all of the Lower Triassic localities examined. These concentrations also maintain a fairly consistent thickness throughout these units, with individual beds varying from pavements to 10s of cm in thickness, although amalgamated packages are rarely more than a meter in thickness. The distribution of shell-bed thicknesses is similar to that of the Jurassic (Kidwell and Brenchley, 1994); although most beds are less than 20 cm in thickness, some beds range up to nearly 2 m in thickness. This contrasts with shell-bed measurements from the Paleozoic, where, other than encrinites (Phelps and Droser, 2001), shell beds are consistently less than 1 m thick, with only rare exceptions greater than 50 cm thick (Kidwell and Brenchley, 1994; Li and Droser, 1997, 1999; Boyer and Droser, 2003). Thus, although this is a time of recovery, the impact of abundant bivalves on thicknesses of shell beds is evident already.

Lower Triassic shell beds can be compared to other shell beds throughout the Phanerozoic. These shell beds are dominated by members of the Modern Evolutionary Fauna, particularly bivalves and gastropods (Sepkoski, 1981). Kidwell (1990) suggested that shell beds dominated by

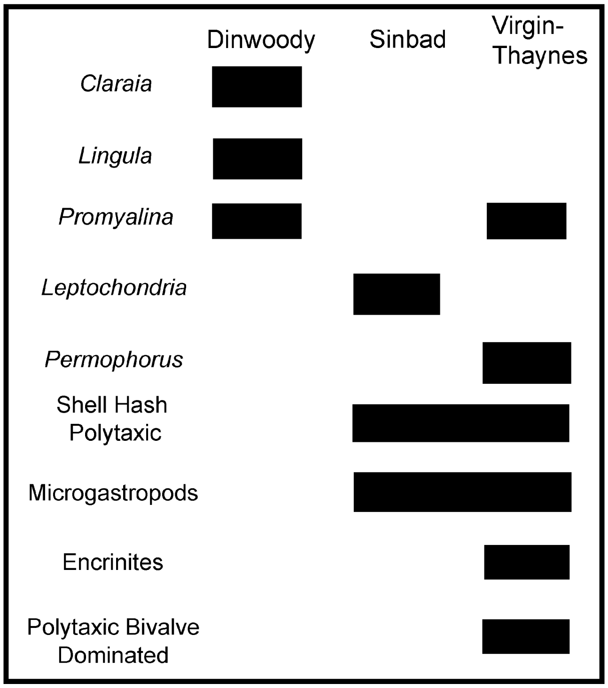

FIGURE 6—Types of shell beds present in each of the three stratigraphic intervals characterized by dominant bioclast contributor. Other taxa occur in these shell beds (see Table 2), but do not dominate shell beds through these intervals.

members of the Modern Fauna with a three-dimensional geometry (>1 m thick) are typical in post-Jurassic strata, whereas pre-Jurassic shell beds commonly are dominated by brachiopods, and are typically thinner and more two dimensional. Although the shell beds in this study are dominated by molluscs, they are relatively thin compared to more modern (post-Paleozoic) shell accumulations that are commonly several meters in thickness (Kidwell, 1990; Kidwell and Brenchley, 1994). This suggests that these Early Triassic fossil concentrations could represent an intermediate in the transition from archaic shell beds of the Paleozoic to post-Jurassic modern shell beds that are taxonomically modern, but geometrically more similar to Paleozoic shell beds (Kidwell, 1990). A recent study (Simões, et al., 2000) suggests that this transition from archaic to modern style preservation of shell beds started as early as the Permian, and was punctuated by the end-Permian mass extinction, which ultimately supports Kidwell's (1990) observation of a phylogenetic rather than environmental mechanism as the primary cause of these modes.

The taphonomic signatures of some of these shell beds support the claim that they represent local or neighborhood communities, and therefore record a meaningful ecologic signature. The taxonomic diversity of bioclast producers, at both the species and higher taxonomic levels, increases through these three Early Triassic time intervals (Fig. 6). In the Griesbachian, shell beds are comprised almost exclusively of the bivalves *Promyalina* and *Claraia* or the brachiopod *Lingula*. The Sinbad Limestone records an increase in taxonomic diversity of bioclasts present in shell beds with significant numbers of microgastropod species as well as more common polytaxic shell beds. In the Spathian, echinoderms first occur as significant contributors to fossil concentrations, forming encrinites and monospecific echinoid spine beds as well as occurring in other polytaxic beds. Despite the increase in the number of bioclast producers contributing to shell beds through the Early Triassic, diversity is still consistently low within these beds (Table 2).

In particular, monospecific shell beds are common in each of these three intervals. True monospecific beds are extremely rare in the fossil record (Alexander, 1977; Thompson and Newton, 1987; Boyer and Droser, 2003), and commonly result either from sorting or from opportunistic species taking advantage of unusual environmental conditions that would be stressful for most species (Levinton, 1970). Quiet-water, low-oxygen settings are commonly the sites of monospecific fossil concentrations (Wignall, 1989). The monospecific concentrations in this study are unusual in that they represent deposition on a mixed carbonate-siliciclastic shelf or carbonate ramp above storm wave base, not in a restricted basinal setting. As a result, there is no sedimentological indication of environmental stress, such as laminated sediments indicating low oxygen, and thus, in these strata, only the biota give any indication of stressful conditions.

Further, while opportunistic blooms commonly are preserved as pavements, indicating brief intervals of variations in environmental conditions (Wignall, 1989), monospecific shell beds in these strata often are more than 10 cm in thickness, suggesting significant intervals of stressful environmental conditions resulting in dominance by exclusively one species. The common occurrence of monospecific beds throughout the Early Triassic is consistent with the suggestion that Early Triassic environments experienced long-term stress (Woods et al., 1999; Bottjer, in press). Environments that are exposed to constant stress for comparable intervals are not found in the modern or any other time in the Phanerozoic, making the Early Triassic a unique time in the history of life.

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