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Echinoid concentration beds: two examples from the stratigraphic spectrum

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Abstract

Echinoid concentrations provide insight into the role of shell composition and taphonomic resilience in the formation of shell bed types. The two groups of echinoids, regular and irregular, have very different responses to taphonomic processes and result in different types of fossil accumulations, on which relatively little previous research has been conducted. Such concentrations provide important information about the preservation of taphonomically fragile echinoid skeletons. To better understand the unique characteristics and depositional histories of echinoid beds, the stratigraphy, sedimentology, petrology and paleontology of two echinoid beds, a sand dollar bed from the Miocene Buttonbed Sandstone of California and a sea urchin spine bed from the Lower Triassic Virgin Limestone of Nevada, were studied. Both the Virgin Limestone echinoid bed and the Buttonbed coquina are nearly monospecific echinoid accumulations and therefore represent extreme examples of echinoid-rich deposits. Similarly, these two beds provide distinctly different examples of fossil echinoid beds because: (1) they are composed of different types of echinoids; (2) they were deposited in different marine environments; and (3) they represent very different stages in the evolutionary history of echinoids. The Buttonbed sand dollar bed, deposited in a shallow marine siliciclastic environment, was formed by both biogenic and sedimentologic processes. In contrast, the Virgin Limestone spine bed, deposited in a distal carbonate shelf setting, was subject to diagenetic as well as biogenic and sedimentologic processes during formation. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

For paleontologists, bioclastic deposits are commonly ‘the key to the past’. Clues within these deposits provide information which enables reconstruction of ancient environments and their depositional histories. Shell beds have been a prominent topic of paleontologic research in recent years (Seilacher, 1982; Kidwell and Jablonski, 1983; Kidwell, 1985,

1991a,b; Kidwell et al., 1986; Davies et al., 1989a,b; Kidwell and Bosence, 1991; Kidwell and Holland, 1991; Ketcher and Allmon, 1993). Such accumulations are very diverse with many forms present in the stratigraphic record. Composition varies greatly within shell beds to include any concentration of invertebrate skeletal parts within a terrigenous or carbonate matrix.

Echinoid-rich accumulations provide insight into the role of shell composition and taphonomic resilience in the formation of shell bed types. The

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two groups of echinoids, regular and irregular, have very different skeletal microstructures. Thus, their response to hydrodynamic forces and subsequent post-mortem survival results in distinct types of fossil accumulations. Because it is relatively difficult to preserve echinoids (particularly regular echinoids; Kier, 1977a; Greenstein, 1993), concentrations of these fossils offer unique insight into the history of the deposits in which they are preserved. The purpose of this paper is to examine the paleontologic, stratigraphic, sedimentologic and petrographic aspects of two such accumulations in order to better understand the unique characteristics of echinoid beds. Taphonomic analysis of the accumulations, in conjunction with stratigraphic, sedimentologic and petrographic information, has enabled us to reconstruct the depositional histories of the beds and to determine the processes which controlled their generation.

1.1. Preservational potential and the echinoid fossil record

There appears to be a preservational bias in the echinoid fossil record which favors preservation of irregular echinoid fossil material over that of regular echinoids. Kier (1977a) documented that the regular echinoid record is poor compared to the irregular echinoid record; only 20% of known echinoids from the Tertiary are regular echinoids whereas today 53% of all living echinoids are regular echinoids. Smith (1984) identified two sources of bias leading to the dramatic difference in preservation potential between the two groups. First, the type of environments that the two groups evolved and diversified in are quite different. Regular echinoids evolved and diversified as grazers and most prefer shallow water firm ground or rocky strata (sites of active erosion which disfavor preservation; Smith, 1984; Barnes, 1987). Irregulars, however, evolved and diversified as deposit feeders and most prefer to live on or in unconsolidated sediments (areas of sedimentation which promote preservation; Smith, 1984; Barnes, 1987).

The second factor which accounts for the difference in preservation potential between the two echinoid groups is the rigidity of their tests. There are a wide variety of test structures found among echinoids with each exhibiting different degrees of

rigidity following the post-mortem decay of connective tissues (Smith, 1984). Preservation potential is greater for those echinoids with a high degree of interlocking between test plates. Overall, regular echinoids tend to have less resilient tests than irregulars. Recent actualistic studies have aided in understanding the disarticulation threshold of regular echinoid test material and have concluded that test resilience is highly variable even within families (Kidwell and Baumiller, 1990; Greenstein, 1990, 1991). Differences in test rigidity, as well as environmental preferences, have changed over the evolutionary history of the Class Echinoidea and as a result, knowledge of post-Paleozoic echinoids is greater than what is understood of the Paleozoic history of this group.

In an actualistic study of live and dead populations of regular and irregular echinoids, Greenstein (1993) found that the majority of irregular echinoid carcasses were located on the substrate suggesting that their infaunal life habit did not remove them from post-mortem taphonomic processes. The author also found a lack of abundant irregular echinoid subfossil material in areas of large live populations. He cited modern ecological studies of sand dollar populations in which high population densities did not result in rich accumulations of subfossil material. One such study, Salsman and Tolbert (1965), reported 10–15 cm high mounds of sand dollars composed of several hundred individuals resulting from a large die-off of the population. The mounds broke down into fragments within three months and later left no trace of the accumulation. From results of his actualistic study and other neontological studies, Greenstein (1993) concluded that life habit and test construction are not the only determining factors in echinoid preservation potential, and that exceptionally echinoid-rich deposits must result from taphonomic processes extrinsic to the echinoids.

1.2. Echinoid concentration beds

As little previous research has been done on the description and interpretation of echinoid concentration beds, it is necessary to provide a list of working terminology regarding echinoid-rich deposits. Here, we expand upon the definition of a shell concentration provided by Kidwell et al. (1986, pp. 228–229,

“any relatively dense accumulation of biologic hard-parts, irrespective of taxonomic composition, state of preservation, or degree of post-mortem modification”), to include relative compositional abundance as a discriminating factor in determining an ‘echinoid-rich deposit’ from an ‘echinoid bed’. An ‘echinoid-rich deposit’ is herein defined as a shell bed in which at least 50% of the megascopic fossil material (greater than 2 mm in diameter) is echinoid material. Within the same classification scheme, an ‘echinoid bed’ is described as a more extreme example of an echinoid-rich deposit in which over 75% of the megascopic fossil material is echinoid material.

Because of the high percentage of taphonomically responsive fossil components within them, echinoid beds can provide particularly important insight into the role of shell composition in the formation of different types of shell beds. This paper focuses on two echinoid beds: an irregular echinoid (sand dollar) bed within the Miocene Buttonbed Sandstone of central California and a regular echinoid (sea urchin) spine bed within the Lower Triassic Virgin Limestone of southwestern Nevada (Fig. 1). The two fossil accumulations provide very different examples of an echinoid bed. They contain different types of echinoids which were deposited in very different environments (siliciclastic vs. carbonate) during different stages in the evolutionary history of echinoids (the diverse prosperous Cenozoic vs. the depauperate slow recovery from the Permian–Triassic mass extinction). Examination of the paleontologic, sedimentologic, stratigraphic and petrographic aspects of these echinoid beds reveals that the two accumulations resulted from different primary processes. The Buttonbed echinoid bed was formed by both biogenic and sedimentologic processes, whereas the Virgin Limestone spine bed was generated primarily by physical agents.

2. Geological context

The Buttonbed sand dollar bed is found within the Miocene Buttonbed Sandstone of the Temblor Formation and is located just west of Buttonwillow, California, at the Chico Martinez Creek or Buttonbed Hill locality (Fig. 1). The echinoid bed is observed within the uppermost portion of the But-

tonbed Sandstone, which is named for its abundant echinoids. The sandstone member can be divided into three shallowing-upward lithofacies: a lower fine-grained bioturbated sandstone, a thick interval of medium-grained, sandwave cross-stratified sandstone, and an upper echinoid coquina. Echinoids are found throughout the lithofacies but are only greatly abundant within the uppermost lithofacies. The three lithofacies represent subenvironments on an early Relizian (17–18 Myr) shelf (Carter, 1985). The lower bioturbated fine-grained sandstone unit represents deposition in quiet waters some distance offshore. The overlying sandwave lithofacies represents continued shoaling as sandwaves migrating south to southwest built up in the early Relizian regression. This shoaling exposed a broad area to high energy shallow marine conditions, such as vigorous current or wave action, which led to the deposition of the coarsest sandstone lithofacies, the Buttonbed echinoid coquina.

In contrast to the Buttonbed coquina, the Virgin Limestone echinoid bed is a sea urchin spine bed. The accumulation is located in the Lower Triassic Virgin Limestone member of the Moenkopi Formation at the Lost Cabin Springs locality in southwestern Nevada (Fig. 1; see Schubert, 1989, for detailed locality information and measured stratigraphic sections). The overall sequence of numerous limestone units and intercalating terrigenous intervals found in the Virgin Limestone member has been interpreted to represent the distal portion of a shelfal setting (e.g. Schubert, 1989). The limestone units themselves comprise a series of fossiliferous beds separated by thin-bedded carbonate mudstones. While the mudstones show signs of horizontal bioturbation, physical reworking and pressure solution, the fossiliferous units are typically devoid of sedimentary structures and may have erosive boundaries with the surrounding mudstones, suggesting that they are distal storm deposits (Schubert, 1989).

Within the Virgin Limestone member at Lost Cabin Springs, the echinoid bed is part of a shallowing-upward carbonate succession. In most sections, it is underlain by a series of laminated beds, which appear devoid of macrofossils, and overlain by a microgastropod-rich limestone. The echinoid bed is part of a larger dark gray limestone unit, which ranges in thickness between 1.46 and 2.80 m and is relatively

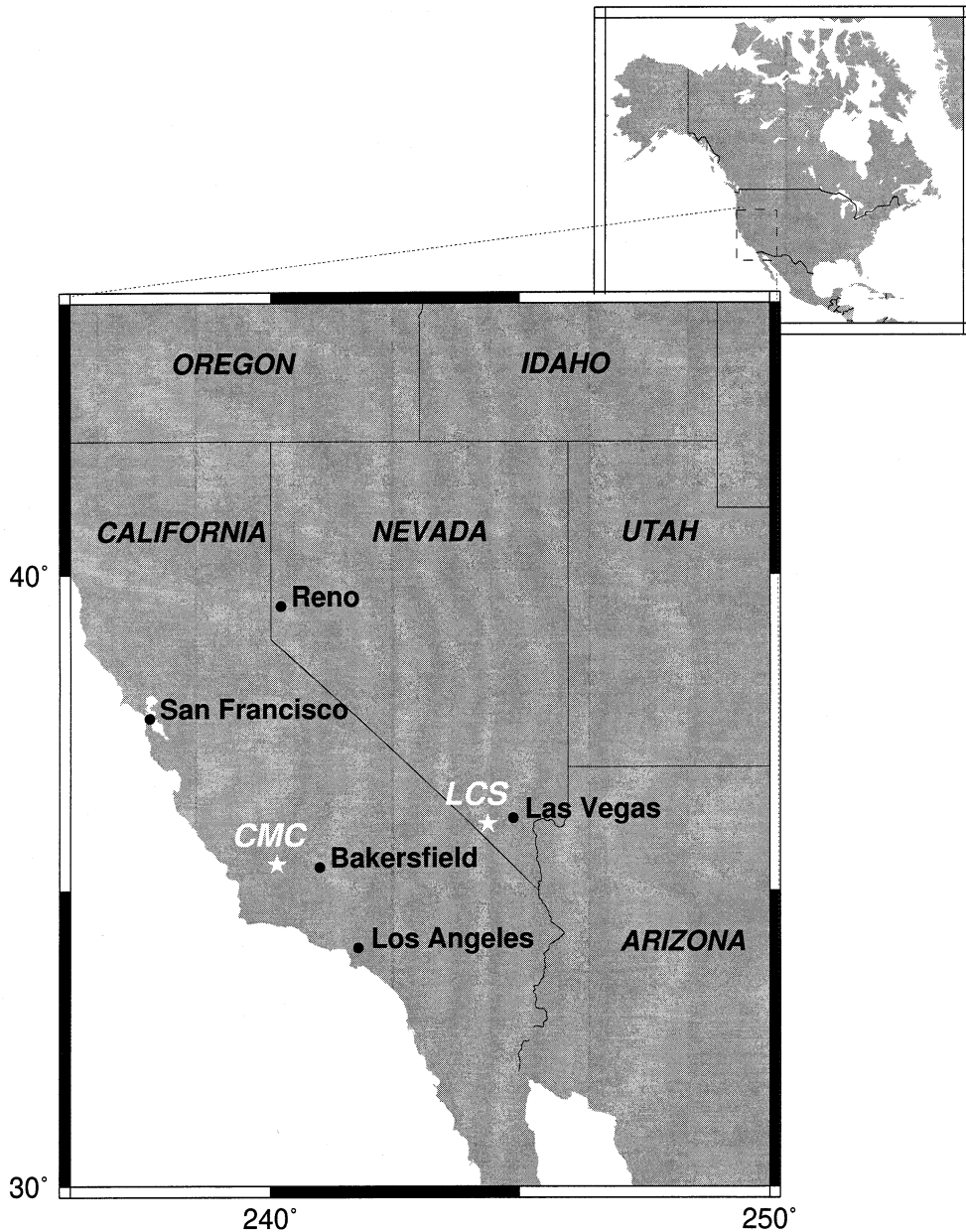


Fig. 1. General locality map of the two echinoid bed study sites. *CMC* = Buttonbed Sandstone echinoid bed at Chico Martinez Creek, CA. *LCS* = Virgin Limestone echinoid bed at Lost Cabin Springs, NV.

uniform in shape. At its base, the larger unit comprise 25–30 cm of unfossiliferous limestone overlain by one to three laterally extensive black chert layers. The cherts range in thickness between 1.5 and 2.5 cm and are each separated by 10 cm intervals of un-

fossiliferous limestone. The cherts are massive and show no internal sedimentary structures. Above the cherts lies the echinoid accumulation, which ranges in thickness between 1.15 and 2.5 m.

3. Methods and material studied

In order to assess the stratigraphy of the echinoid beds, vertical sections of the beds were measured and recorded at stations along each accumulation (nine stations at Chico Martinez Creek and five at Lost Cabin Springs; see Moffat, 1996, for detailed locality information). At each site, lithologic features (color, composition, friability, etc.) and changes in weathering profile were recorded. Also, general lithologies of the surrounding facies were noted and contacts above and below the echinoid beds were examined and recorded in graphic logs.

Sedimentary and ichnological structures were also examined and recorded in the field. The relationship of size and abundance of body fossils to matrix (material less than 2 mm) were described. Packing and sorting of fossils within the units were determined using Kidwell and Holland's (1991) schematic scale of relative packing (densely packed, loosely packed, dispersed). Variations in packing and sorting distributions (both vertically and horizontally) throughout the stratigraphic sections were described at each station.

In the field, paleontologic observations were based on surface exposures. Fossil composition, diversity and abundance were described for each section. All fossil elements greater than 2 mm were point-counted using a stratified random sampling scheme (see Moffat, 1996, for details on sampling). In the Buttonbed coquina, only sand dollar material in which the tests' diameters could be observed were considered 'whole specimens'. Also, taphonomic condition as well as fossil orientation relative to bedding were recorded. In particular, degrees of ornamentation (e.g. presence of petal structure in Buttonbed sand dollar specimens, presence of longitudinal striations on Virgin Limestone spines) were noted. Multiple samples (37 from the Buttonbed Sandstone, 26 from the Virgin Limestone) were collected from beds at each station site, including samples throughout the echinoid beds and a few from the surrounding units at some stations.

In the laboratory, samples were examined for fossil composition and abundance to supplement field observations (see Moffat, 1996, for details). Relative packing of fossils and orientation patterns (relative to original bedding) were described. Orientation of

spines within the Virgin Limestone echinoid bed was determined by noting the general longitudinal directions (e.g. perpendicular/parallel to bedding) of individual specimens and recording any directional trends observed in more than 50% of specimens from each sample. Degrees of ornamentation and breakage among specimens were described using a qualitative 3-point scale to determine the taphonomic condition of the spines observed in the Virgin Limestone echinoid bed: (1) well preserved with striations; (2) some striations present; and (3) smoothed or abraded surface with no striations present.

Petrographic information was obtained by examining thin sections made from several samples from each locality. Fossil abundance was determined through visual estimations of the percent-volume of fossils within the rocks using percent-volume charts, such as those provided by Schäfer (1969) and Kidwell and Holland (1991). Relative sorting of fossil material was also noted. In addition, petrographic analysis of each bed provided information about size variability of fossils throughout the beds, degree of rounding of skeletal grains, and possible orientation of fossil material relative to bedding. Slides from each sample were also examined to determine sedimentological aspects of the rocks, including matrix composition, porosity, the ratio of grains to matrix, and degree of diagenesis of the rocks.

4. Results

4.1. Buttonbed sandstone echinoid bed

4.1.1. Stratigraphy and sedimentology

The Buttonbed coquina is lenticular in nature, with a maximum thickness of 4.1 m in outcrop. In general, the echinoid bed can be divided into two subunits: a coarse upper hash layer which caps the sandstone member and a lower layer composed of more complete sand dollars (Fig. 2). Within the measured sections which exhibit both subunits, the upper hash unit ranges in thickness between 0.65 and 2 m while the lower specimen-rich unit ranges from 1 to 2.5 m thick. There is a sharp contact between the two subunits which is marked, in some areas, by concentrated lag deposits. Fossils within the very closely packed intervals are predominantly

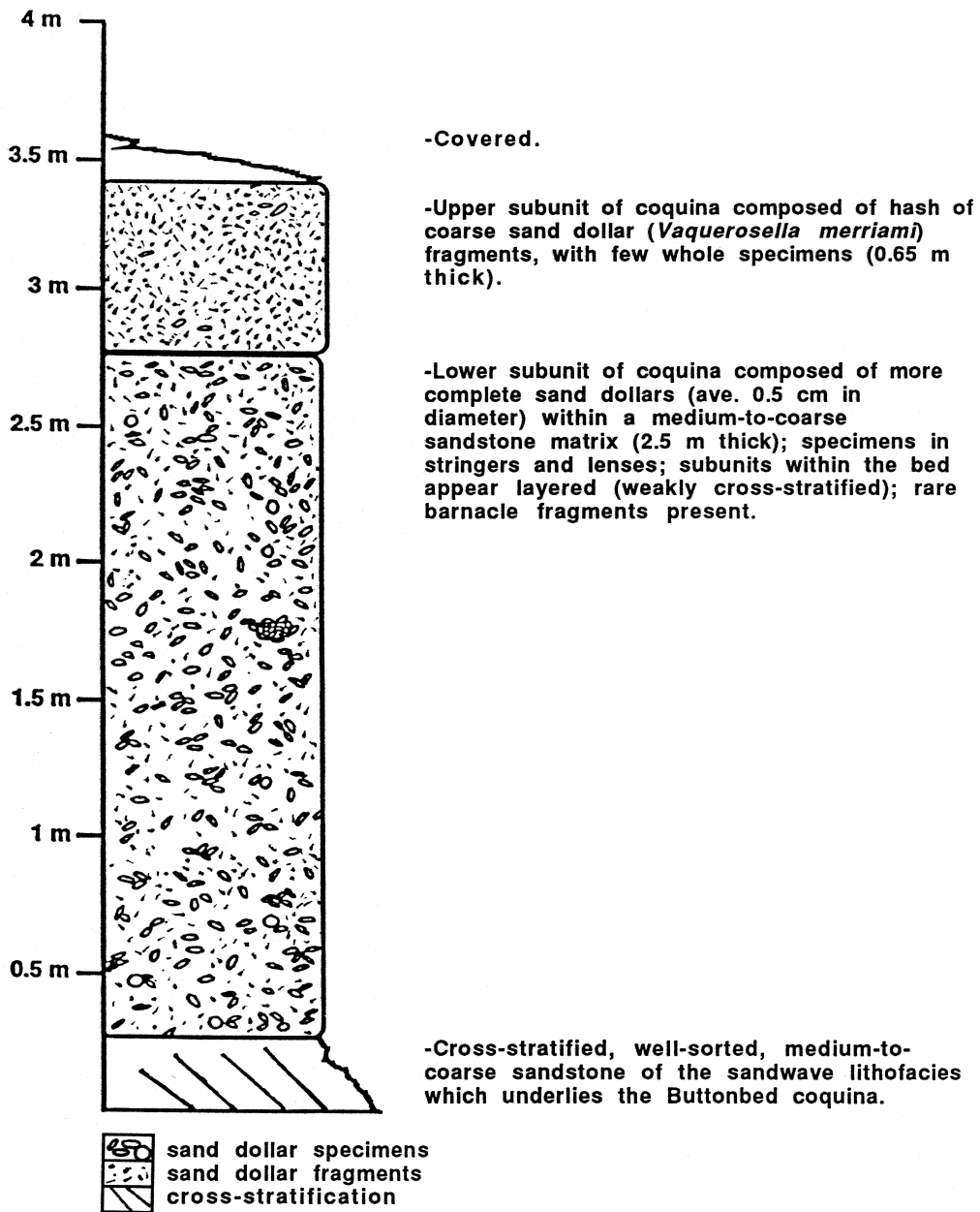


Fig. 2. Schematic stratigraphic section of the Buttonbed Sandstone echinoid bed at the Chico Martinez Creek locality. Scale is in meters.

horizontal relative to bedding and show little signs of taphonomic destruction (e.g. sutured plates and petal structures are present in pristine condition).

Trough cross strata sets with amplitudes of 5 to 20 cm and rare tabular sets with amplitudes of 20 to 40 cm are found within this echinoid bed (Carter, 1985).

Physical sedimentary structures present within the lower portion of the coquina include rare small scale lenticular lag deposits which project below the usual lower surface of the bed and are commonly infilled with sand dollar tests. These lag 'holes' average 1 to 2 m in length and 5 to 10 cm in depth. Tests are not

oriented in any consistent direction within the lag holes, suggesting rapid infill due to storm activity.

Other small scale structures within the lower subunit of the Buttonbed echinoid concentration include several specimens of an unnamed, vertical, conical burrow. These are typically 15–20 cm deep, 5–15 cm in diameter, commonly infilled with coarser sand, and are located near the base of the coquina. All recognizable traces are vertical and have been assigned to the *Skolithos* ichnofacies, indicating a high-energy marine paleoenvironment (Carter, 1985).

Dark brown, granule-sized (1–4 mm) phosphatic nodules are scattered throughout the echinoid bed, with several concentrated zones. Nodular phosphorite typically forms in reduced, organic-rich offshore environments (Tucker, 1991; Williams et al., 1982). The abundance of phosphatic nodules present in the sandstone suggests proximity to their place of origin; the concentrations of phosphatic nodules probably represent allochthonous storm deposits (Carter, 1985). The nodules most likely formed in quieter deeper marine surroundings and were later exposed and transported by storm activity.

4.1.2. Sedimentary petrology

On the petrographic scale, the Buttonbed echinoid bed's non-skeletal composition is predominately quartz (averaging 25% volume), with smaller amounts of glauconite (5%) and feldspars (less than 1%). Quartz grain sizes vary between 0.05 and 2 mm and show no size distribution patterns (i.e. coarsening or fining upward) or evidence of preferential sorting. Glauconite grains can be observed as both nodules and ooids, which display a spectrum of weathering stages ranging from 'fresh' characteristically green aggregates to dark brown limonitic aggregates resulting from oxidation. The pellets and ooids range in size from 0.05 to 0.9 mm in diameter. Degree of rounding of grains varies throughout the bed, with no apparent pattern. Overall, there was no evidence of consistent orientation of clasts within the examined thin sections, with the exception of a concentrated scallop shell layer observed between the bed's two subunits on one small portion of the bed. The percent volume of grains to matrix averaged 50% for the bed. Mineral grains and fossil material are surrounded by a matrix of microcrystalline calcite.

Fossil components examined in the thin sections include fully articulated sand dollar tests (with pillar structures visible), echinoderm debris, bryozoan and barnacle fragments, bivalve debris, and rare microgastropods and benthic foraminifera. Fossil material accounted for 5–35% of the petrographic field-of-view. Sand dollar tests have been completely recrystallized by coarse calcite crystals which have each replaced the individual echinoid plates (they lack any signs of original internal structure). Plate suturing is still observable in test cross sections, and calcite syntaxial overgrowths on echinoderm debris are quite common.

4.1.3. Paleontology and discussion

The echinoid bed is dominated by the button-like sand dollar, *Vaquerosella merriami*. These irregular echinoids range in size from 0.5 to 2 cm in diameter. The only other macrofaunal components observed in the Buttonbed coquina at the Buttonbed Hill locality are scallop shells and occasional fragments of an unidentified barnacle. Scallops (possibly *Leptopecten andersoni*) are found in low abundance scattered throughout the coquina and within one densely concentrated zone (6 cm thick) located on one small hill at the locality.

Fossil abundance and distribution vary both vertically and laterally within the Buttonbed echinoid bed, with sand dollar specimens composing up to 80% volume in some outcrop areas. Abundance of *V. merriami* within the echinoid bed suggests that these organisms lived in great numbers (for many generations) in the area and were only affected by moderate transport. Fossil abundance analyses (specimens per 100 cm²) show a decrease in sand dollar specimens found in the lower subunit versus those from the upper hash subunit (Table 1). The overall pattern of decreasing abundance of sand dollar tests upsection within the Buttonbed coquina accompanied by an increased abundance of fragments indicates a significant amount of reworking of the fossil material as time progressed. The combination of progressively shallower marine high energy conditions with periodic storm-intensified reworking led to an increase in test destruction. The ever-present overwhelming abundance of *V. merriami* within the bed supports the conclusion that changes in specimen abundance within the bed were the result of physical, and not

Table 1

Results of fossil abundance and packing of the Buttonbed Sandstone echinoid bed

Station (No.)	Sampling position	Abundance (per 100 cm ²)	Packing	Packing (w/fragments)	Station (No.)	Sampling position	Abundance (per 100 cm ²)	Packing	Packing (w/fragments)
B1 (BA)	(1) base	20	DIS	D	B6	(1) 20 cm up	3	DIS	D
	(2) 20 cm up	16	DIS/L	D		(2) 20 cm up	11	D/L	D
	(3) 20 cm up	19	DIS/L	D		(3) 20 cm up	0	–	D
	(4) 20 cm up	22	DIS/L	D		(4) 20 cm up	9	D/D/L	D
	(5) 20 cm up	6	DIS	D		(5) 20 cm up	10	L	D
						(6) 20 cm up	9	L	D
B2	(1) 20 cm up	14	DIS	D	(7) 20 cm up	1	L/D/D	D	
	(2) 20 cm up	4	DIS	D	(8) 20 cm up	1	–	D	
	(3) 20 cm up	2	DIS	D	(9) 20 cm up	5	DIS	D	
	(4) 20 cm up	2	DIS	D	B7	(1) 10 cm up	11	L/DIS	D
	(5) 20 cm up	0	–	D		(2) 20 cm up	7	L/DIS	D
				(3) 20 cm up		23	L/D	D	
B3	(1) base	0	–	D	(4) 20 cm up	5	L/DIS	D	
	(2) 20 cm up	5	DIS	D	(5) bet. 3 and 4	39	D/D/L	D	
	(3) 20 cm up	1	DIS	D	B9	(1) base	10	DIS	D
	(4) 20 cm up	13	DIS/L	D		(2) 20 cm up	0	–	D
	(5) 20 cm up	8	DIS	D		(3) 20 cm up	0	–	D
	(6) 20 cm up	2	DIS(L)	D		(4) 20 cm up	0	–	D
	(7) 20 cm up	0	DIS	D		(5) 20 cm up	5	DIS	D
	(8) 20 cm up	4	DIS	D		(6) 20 cm up	2	DIS	D
	(9) 20 cm up					(7) 20 cm up	9	L/DIS	D
	(10) 20 cm up	0	–	D		(8) 20 cm up	6	D/D/L	D
	(11) 20 cm up	0	–	D	B10	(1) base	3	DIS	D
	(12) 20 cm up	0	–	D		(2) 20 cm up	18	D/D/L	D
	(13) 20 cm up	0	–	D		(3) 20 cm up	5	DIS	D
				(4) 20 cm up		0	DIS	D	
B4	(1) base	7	L/DIS	D	(5) 20 cm up	7	L/DIS	D	
	(2) 20 cm up	4	DIS	D	(6) 20 cm up	0	–	D	
	(3) 20 cm up	17	DIS	D	(7) 20 cm up	0	–	D	
	(4) 20 cm up	0	DIS	D					
B5	(1) base	4	DIS	D					
	(2) 20 cm up	4	DIS	D					
	(3) 20 cm up	3	DIS	D					

Fossil abundance was determined by point-counting sand dollars within a 100 cm² grid at each vertical position (at 20 cm intervals) in a randomly selected portion of each station. Packing was measured within each grid view using Kidwell and Holland's (1991) scale of relative packing: dispersed (DIS), loosely packed (L) and densely packed (D). The 'Packing' column accounts for relative packing of specimens only, whereas the 'Packing (w/fragments)' column considers both specimens and sand dollar fragments (1–3 mm). Within some stations, horizontal lines delineate samples from the lower subunit (above line) and the upper hash subunit (below line). For station location information, see Moffat (1996).

biological, factors. The sand dollars are present in the underlying sandwave interval, suggesting that the fossils are not specific to the echinoid bed alone. Their great abundance within the coquina, combined with the winnowed fabric of the bed, point to a strong physical control on the final deposition of the

echinoid bed. The relatively shallow marine paleoenvironment suggested by sedimentologic data (Carter, 1985) would have been much affected by high energy processes, particularly during storm events.

Although some lenses and stringers of sand dollar tests appear to have been deposited horizontal



Fig. 3. A poorly sorted portion of the Buttonbed Sandstone echinoid bed. Specimens range from 0.5 to 2 cm in diameter.

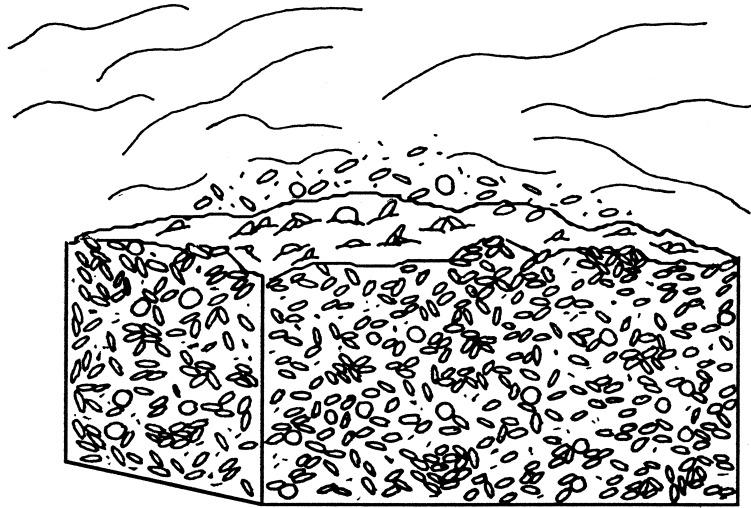
to the bedding plane, the majority of fossil material in the Buttonbed echinoid bed was not deposited in any consistent orientation. Most of the *V. merriami* specimens observed in the bed appear jumbled together, deposited in every direction relative to the seafloor surface, indicating that the accumulation is the product of significant reworking and not an intact paleocommunity.

In general, packing of *V. merriami* within the echinoid bed is highly variable, both laterally and vertically (Table 1). Densely packed areas and more dispersed areas with occasional lenses and stringers were observed. When the presence of sand dollar fragments (1–3 mm in size) is considered, the degree of packing of the accumulation changes dramatically. Every observed outcrop exhibiting a dispersed sand dollar test fabric was reclassified as a densely packed accumulation when sand dollar fragments were taken into account; the Buttonbed coquina represents a dense concentration of sand dollar material. The dense packing of this coarse-grained echinoid bed is indicative of winnowing events which removed the

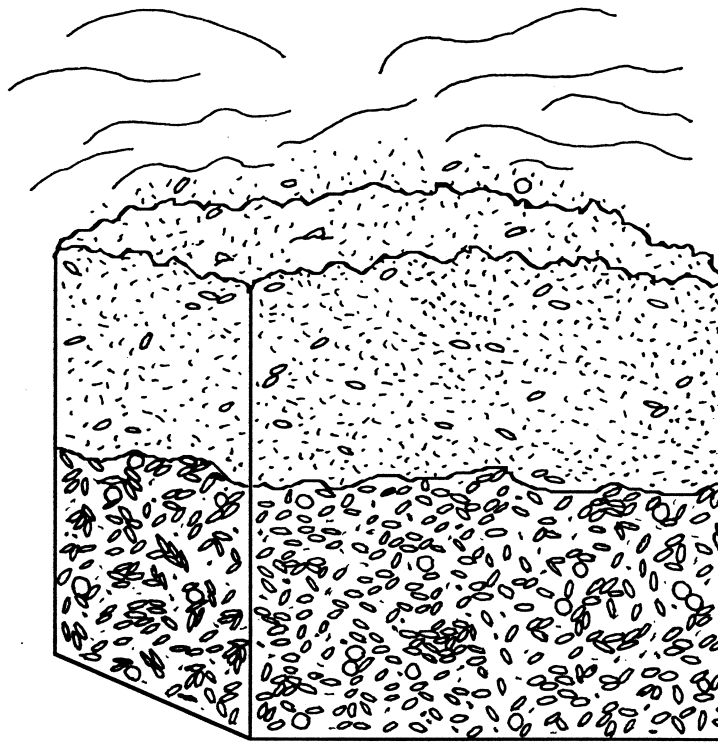
finer grained material from the area and reworked the coarser fossil material, packing it together.

Within the bed, sorting of fossil material is also highly variable, both laterally and vertically (Fig. 3). In fact, well-sorted areas with sand dollar tests of approximately equal size and poorly sorted areas with tests ranging from 0.5 to 3 cm in diameter can be found in close proximity in some portions of the bed. Overall, no sorting pattern could be distinguished.

Taphonomic condition of the fossils varied greatly throughout the bed. It should be noted that the majority of sand dollars examined in the accumulation are present in cross-section only. This view made taphonomic assessment very difficult, except to note that the sand dollar tests were intact enough to preserve a cross-sectional view. The specimens of *V. merriami* which are present with observable aboral or oral views exhibit a variety of preservational states, ranging from those which are relatively 'pristine' (with original petal structures and individual sutured plates still visible) to specimens that have



A.



B.

Fig. 4. Reconstruction of the depositional history of the Buttonbed Sandstone echinoid bed. (A) High energy conditions, such as current winnowing and storm events, rework the shallow marine environment. The abundant sand dollar tests are deposited in a variety of stratigraphic and taphonomic styles. (B) Additional reworking of the material results from further current winnowing as the shelfal environment continues to become shallower.

completely smoothed surfaces and breakage across plate boundaries. Overall, the taphonomic conditions of the specimens exhibiting aboral or oral views indicate signs of multiple reworking, perhaps by sandwave or current winnowing, with fewer well-preserved specimens among the majority of heavily abraded individuals. The taphonomy of the Buttonbed echinoid bed supports the conclusion that the echinoid concentration was affected by periodic storm-intensified events which incorporated many generations of *V. merriami* into a winnowed, coarse-grained fossiliferous deposit.

4.1.4. Summary

The Buttonbed echinoid bed was formed in a relatively shallow marine environment, as is indicated by paleontologic, sedimentologic and stratigraphic evidence. During Relizian times, the Buttonbed area was a shelf environment that experienced further shallowing during deposition of a sandwave interval, which preceded deposition of the coquina. Populations of *V. merriami* thrived in the surroundings for many generations. High energy conditions, such as storm events and winnowing by current action, produced the generally jumbled accumulation observed in the lower portion of the Buttonbed coquina (Fig. 4). The complexity of this subunit of the concentration bed suggests that it is the result of multiple reworking events, which preserved the massive amount of sand dollar material in a variety of stratigraphic and taphonomic styles. Additional reworking of the overlying hash subunit probably occurred as a result of current winnowing, the product of an increasingly shallower marine environment.

4.2. Virgin limestone echinoid bed

4.2.1. Stratigraphy and sedimentology

The Virgin Limestone echinoid bed is part of a thicker dark gray limestone unit (Fig. 5). Spines first appear approximately 20 to 30 cm above the uppermost chert layer and remain present throughout the rest of the unit. It is important to note that, with the exception of the chert layers, the echinoid spines are the only macroscopic features observed in this limestone unit; no other physical or biogenic structures were found. Lack of obvious bioturbation within the unit strongly contrasts with the bioturbated nature of

many of the carbonate mudstones within the Virgin Limestone member. It has been suggested that the lack of biogenic and sedimentary structures within this limestone unit indicates that it was deposited as a storm bed (Schubert, 1989).

4.2.2. Sedimentary petrology

Petrographically, the echinoid bed is a matrix-supported fossiliferous limestone comprising echinoid spines, echinoderm debris, bivalve fragments and rare microgastropods. Fossil abundance ranges from 25 to 45% (predominantly echinoderm material), fossil material ranges in size from 0.3 to 7.5 mm, and sorting varies greatly within the samples. Most fossil debris exhibits rounded edges, suggesting reworking of material.

The echinoid spines have been recrystallized to coarse calcite and are surrounded by ragged quartz, indicating surficial silicification of the material. Calcite syntaxial overgrowths on echinoderm debris are quite common. Small stylolites are also present in some samples with glauconite concentrated along them, suggesting the original presence of argillaceous material. Other than its concentration along stylolites, the mineral glauconite is very rarely present within the samples, accounting for less than one percent of their volume. Although there does not appear to be any sedimentological evidence for orientation within the slides (e.g. no geopetal structures), many of the bivalve fragments are oriented parallel to the bedding plane, suggesting that environmental conditions (on the microscopic scale) allowed for settling of the delicate skeletal material.

4.2.3. Paleontology and discussion

Macroscopically, the Virgin Limestone echinoid bed is a monospecific spine accumulation (Fig. 6). Interestingly, the regular echinoid spines which compose the fossil bed appear to belong to an undescribed species of Early Triassic echinoid. This is not highly unusual considering the patchiness of the Triassic echinoid fossil record. In fact, the vast majority of Triassic type species of *Cidariidae*, the only echinoid family traditionally thought to have survived the Permian–Triassic mass extinction, is described from spine material (Greenstein, 1992). Articulated test material is rarely preserved among early post-Paleozoic echinoids because many

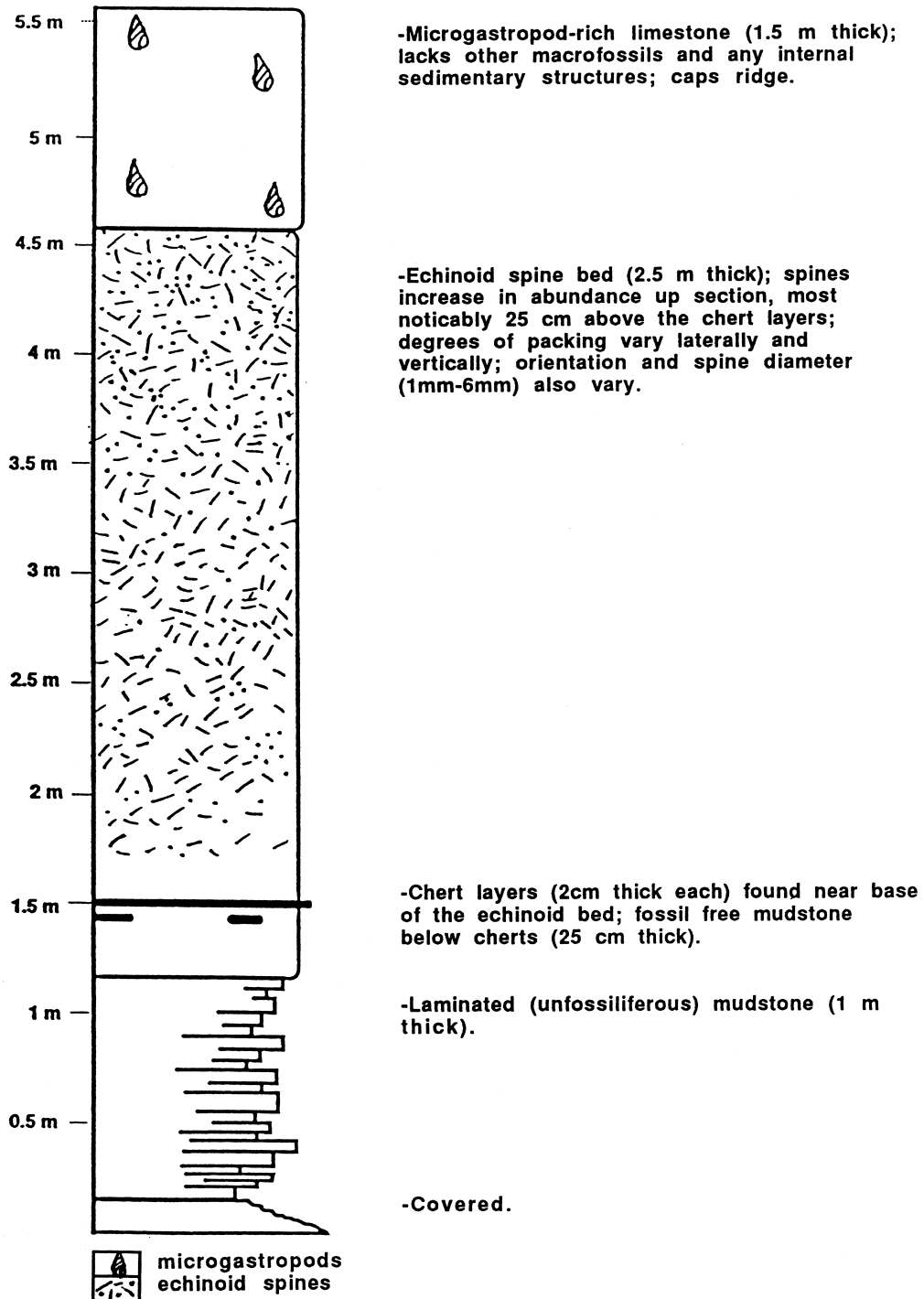


Fig. 5. Schematic stratigraphic section of the Virgin Limestone echinoid bed at the Lost Cabin Springs locality. Scale is in meters.

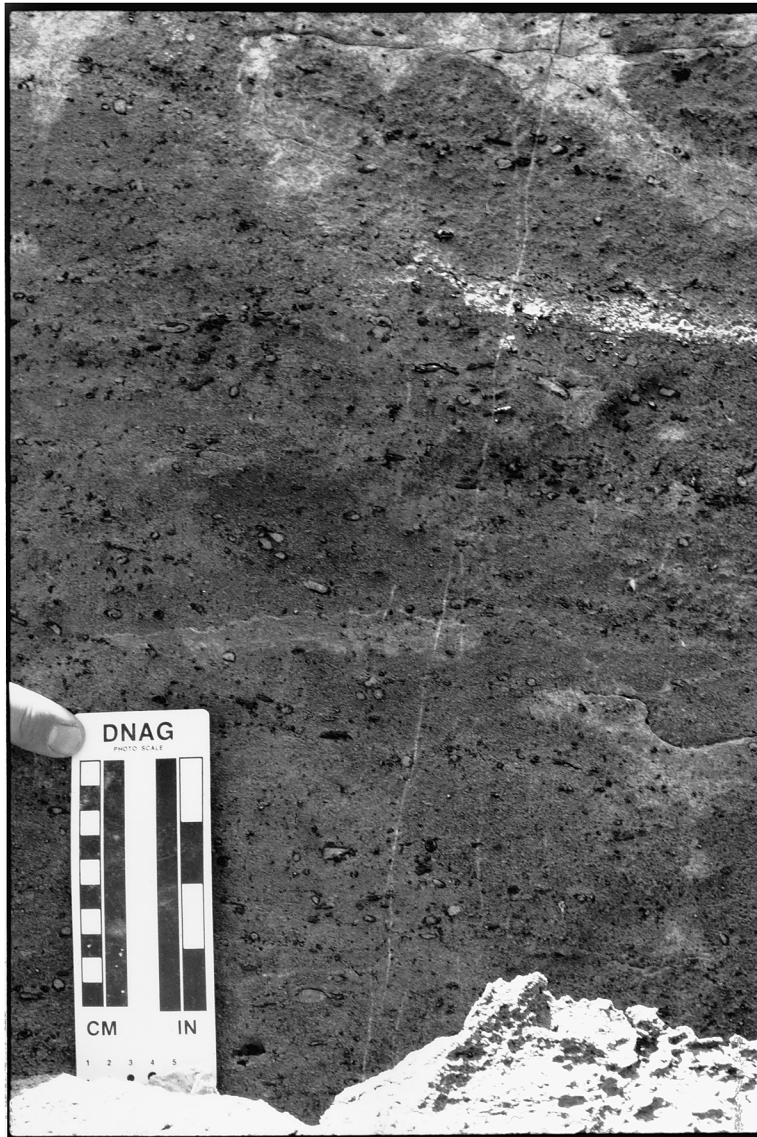


Fig. 6. Photograph of the Virgin Limestone echinoid bed. Note the distribution and silicified nature of the spines within the monospecific accumulation.

of them had imbricated tests, which disarticulated rapidly after death (Smith, 1990). Thus, it is to be expected that spine material would be predominant in fossil assemblages involving these taphonomically fragile early post-Paleozoic echinoids. Spines are among the most resilient skeletal components of the regular echinoid test and would remain intact while more taphonomically fragile test material was disarticulated. Moderate reworking in a depositional

setting would preclude preservation of articulated test material without inhibiting spine preservation.

Presently, two species of *Miocidaris* are the only documented echinoids from the Early Triassic (Smith, 1990, and references therein). The spines within the Virgin Limestone bed at Lost Cabin Springs differ significantly from those of the two described species. These spines range from 1 to 6 mm in diameter. Where spine tips are present, the

Table 2
Results of fossil abundance, packing and taphonomic condition of the Virgin Limestone echinoid spine bed

Sample (No.)	Packing	Abundance (per 25 cm ²)	Degree of ornamentation
1A	–	0	–
1B	–	1	3
1C.1	DIS	13	2
1C.2	DIS	18	3
2A	DIS	3	3
2B	DIS	14	3, 2
2C	–	0	–
3A.1	–	1	3
3A.2	DIS	3	3
3B	–	0	–
3C	–	0	–
4A	L	4	3
4B	–	0	–
4D	L	34	3
5A	DIS	19	3
5B	L	20	3, 2
5B+	DIS	10	3
6A	–	0	3
6B	DIS	13	3, 1

Fossil abundance for each sample was determined by point-counting spine material within a 25 cm² quadrant view randomly selected from a 100 cm² grid which was placed on each sample. Degree of ornamentation was based on the degree of preservation of longitudinal striations present on spine material observed within the 25 cm² view. Degree of ornamentation scale: 1 = well preserved with striations; 2 = some striations present; and 3 = smoothed or abraded with no striations present. For sample locality information, see Moffat (1996).

spines appear to taper gently to a terminal point. Longitudinal striations are observed on some of the relatively pristine specimens.

Overall, spines increase in abundance upsection within the echinoid accumulation (Table 2). Field observations record high variability in spine distribution both laterally and vertically within the unit, with occasional densely packed lenses and stringers present among more dispersed areas. Spines appear to be poorly sorted, with various diameters (1–6 mm) visible in outcrop. This range of spine sizes may indicate the presence of several types of spines or may simply be an artifact of examining a two-dimensional view. Identical spines would display varying diameters depending on which portions were cut. As

a result, sorting may appear poorer than it actually is due to the nature of the observed view.

The Virgin Limestone echinoid bed spines were not deposited in any consistent orientation with respect to the bedding plane. Uncommon horizontally bedded stringers are present in the bed but the vast majority of the fossil material shows no consistent trend. This common jumbled appearance suggests that the formation of the spine bed was influenced by significant reworking of the seafloor. Some spines are even oriented perpendicular to the bedding plane. Lack of orientation relative to the bedding plane could have resulted from either a relatively high energy physical process (e.g. storm activity; see Middleton, 1967; Greensmith and Tucker, 1969; Kidwell, 1991b) or bioturbation. It is unlikely that the apparently random orientation of spines within the bed is a product of bioturbation, since many of the smaller, more fragile bivalve fragments surrounding the spines (as seen in thin section) appear oriented parallel relative to the bedding plane, apparently unaffected by local mixing.

Taphonomic analysis of the Virgin Limestone bed spines shows that most of the examined spines are well abraded with no visible longitudinal striations (Table 2). However, various degrees of abrasion occur, and relatively pristine spines are mixed with the more abundant abraded spines.

Spines within the Virgin Limestone bed exhibit variable diagenetic alteration: larger spines (greater than 2 mm in size) have been preferentially silicified. Ragged cryptocrystalline silicification has replaced the outer portions of the larger carbonate fossil material. The immediate source of silica for the echinoid bed is most likely the underlying chert layers. The partially silicified spines on the weathered surfaces of the unit are the only macroscopically diagnostic feature of the bed, producing a distinctive weathering pattern.

All the larger spines observed in thin section and in hand sample appear to be surficially silicified and there is no increasing or decreasing trend in silicification of other fossil material. This suggests that the distribution of silicified material is not the result of the specimen's position relative to the underlying chert. Apparently, the larger spines were preferentially silicified according to their size and not due to a silicification gradient within the echinoid bed.

If the abundance of silicified spines was related to a silicification gradient, it would be expected that a decrease of silicified material upsection would be observed. Primary skeletal structure has been shown to play an important part in the determination of silicification sites (Elorza, 1987; Crowley, 1988; Carson, 1991; Tucker, 1991). The large crystal size of the spines may have caused a cryptocrystalline crust to form, as the carbonate material was dissolved more slowly than silica was precipitated (see Holdaway and Clayton, 1982; Carson, 1991).

4.2.4. Summary

The Virgin Limestone echinoid bed most likely represents a storm debris bed which was deposited onto the distal portion of a shelf setting. Many of the fossiliferous limestone units of the Virgin Limestone at Lost Cabin Springs have been identified as distal storm deposits (Schubert, 1989; Schubert and Bottjer, 1995). Overall, the Virgin Limestone units display several characteristics described in the storm bed literature including intraclasts, erosional boundaries, gutter casts, the absence of internal sedimentary structure, and concave-down bivalve orientation (Schubert, 1989; Schubert and Bottjer, 1995; see summary of storm bed descriptions in Kriesa, 1981; Norris, 1986; Parsons et al., 1988). The echinoid bed is thicker than most of the described storm beds from Lost Cabin Springs but its size has been interpreted to reflect the magnitude of the storm which deposited it (Schubert, 1989).

Although the Virgin Limestone spine bed does not display some of the classic signs of storm bed deposition, such as rip-up clasts, it does exhibit evidence of high energy depositional conditions. The echinoid bed has an erosional base, separating it from the underlying bioturbated mudstone unit. Lack of internal sedimentary structures within the bed also is indicative of some storm beds (Kriesa, 1981; Kidwell, 1982; Aigner, 1985; Norris, 1986). Petrographic analysis reveals that many of the bivalve fragments observed in the bed are oriented parallel to the bedding plane, suggesting that this lack of sedimentary structure is not due to homogenization of the deposit by bioturbation. Active bioturbation would affect the orientation of both the spines and the bivalve material surrounding them. With this petrographic evidence in mind, lack of spine orientation

appears to be the result of physical processes and not the result of movement by bioturbation. Perhaps the difference in orientation patterns between the spines and the delicate bivalves is a result of the different sizes and densities of the two fossil types. The less dense, smaller bivalve fragments would have been hydrodynamically different from the large spines.

The accumulation represents a mix of allochthonous echinoid material and parautochthonous fossil debris [e.g. delicate, thin-shelled bivalve fragments; see Aigner (1985) and Schubert (1989)]. Regular echinoids tend to prefer shallow water, firm ground or rocky strata (Smith, 1984; Barnes, 1987). It is likely that the spines were brought into the depositional area from the shallower eastern part of the shelf. The spine bed is the only portion of the Virgin Limestone at Lost Cabin Springs which exhibits echinoid spine material, supporting an allochthonous origin.

Examination of the taphonomic condition of the spines suggests that the spine bed was composed of fewer relatively pristine specimens among more abundant heavily abraded individuals. This could be the result of differential abrasion due to storm activity or more probably reflects a time-averaged deposit including both significantly reworked material and fresher material.

The amount of matrix and fine-grained fossil material (≤ 2 mm) within the bed suggests that the accumulation was not greatly physically reworked (e.g. winnowed) after deposition. This would seem logical as the energy regime within the distal portion of the shelf is typically low (see onshore-offshore storm bed morphologies in Kidwell et al., 1986; Norris, 1986; Parsons et al., 1988). The echinoid bed was probably deposited from the east into the quieter, deeper setting below normal wave base.

5. Discussion

The two echinoid concentrations described in this paper provide very different examples of echinoid beds and how they form. There are many ways in which the two beds vary, the most prominent being: (1) they are composed of different types of echinoids; (2) they were deposited in different marine environments; and (3) they are from very different stages in the evolutionary history of echinoids. The

following discussion addresses these differences between the two examined echinoid beds and outlines the primary factors which influenced the formation of the beds.

5.1. Echinoid type

As mentioned in the introduction of this paper, the echinoid fossil record documents that different echinoid test morphologies have different degrees of post-mortem resilience. Two end members on the spectrum of test strength are present in the Buttonbed Sandstone and the Virgin Limestone. Clypeasteroids, which include sand dollars, have the most well-structured or resilient tests of all the echinoids, with interlocking sutured plates and supportive internal pillars (Seilacher, 1979; Smith, 1984; Donovan, 1991). *Vaquerosella merriami*'s test enabled it to withstand relatively high energy regimes during life and proved fairly resistant to post-mortem taphonomic processes.

In contrast to the test morphology of the sand dollar, the regular echinoid test is very susceptible to taphonomic destruction (Kier, 1977a; Smith, 1984; Donovan, 1991; Greenstein, 1991). The Triassic was a time in which regular echinoid test structures were evolving from the imbricated variety to more rigid designs (Kier, 1977b; Smith, 1990; Smith and Hollingworth, 1990). Both described regular echinoids from the Early Triassic had imbricated tests (Durham and Melville, 1957; Kier, 1974, 1977b; Smith, 1984). Although no articulated test material was found in relation to the Virgin Limestone spines at Lost Cabin Springs, it can be inferred that the corresponding tests were probably imbricated. These early post-Paleozoic echinoid tests would have disarticulated soon after death when decay and/or scavengers had removed the connective tissue joining the test plates. The more taphonomically resilient parts of the echinoids, the spines, are the only intact macroscopic evidence of the presence of regular echinoids in the Virgin Limestone at Lost Cabin Springs.

5.2. Depositional environment

The fossil components of the two echinoid beds strongly reflect the relative preservational potential

of the two types of echinoids, particularly considering the different types of environments in which the echinoids were deposited. The Buttonbed coquina was formed in a shallow marine siliciclastic environment, as is evident in the stratigraphic and sedimentologic analysis of the bed. The echinoid concentration was shaped by current winnowing and periodic storm activity in the shallow setting, producing the coarse-grained fossiliferous deposit. Although sand dollar fragments are abundant within the lower subunit, many of the sand dollar specimens present in this lower portion of the bed remained intact despite the winnowing action. As the environment became increasingly shallow over time, high energy processes continued to rework the concentration, resulting in an upper hash unit.

The carbonate depositional environment of the Virgin Limestone was deeper marine than the siliciclastic Buttonbed and, therefore, was not subject to the same reworking intensity. Presence of microscopic fossil material, such as delicate bivalve fragments, indicates that the bed was not reworked significantly enough to remove the finer material from the accumulation. Horizontal orientation of the bivalve material suggests that the bed was not bioturbated. Lack of any consistent orientation of spine material relative to the bedding plane may be a product of storm deposition. Lack of internal structure, including bioturbation and sedimentary features, in the limestone suggests that the unit was deposited as a storm debris bed.

5.3. Evolutionary timing

The two echinoid beds represent very different stages in the evolutionary history of the Class Echinoidea. The Virgin Limestone spine bed was deposited following the most devastating mass extinction in the history of life. An estimated 90% of all marine genera present in the Late Permian went extinct at the Permian–Triassic boundary (e.g. Erwin, 1993, 1994). As previously mentioned, only one genus of echinoid, *Miocidaris*, is reported for Early Triassic times. This was a crucial time of recovery for the class. It is also a time in the evolutionary history of echinoids that is poorly understood by paleontologists. Knowledge of the echinoid fauna of the Early Triassic is very patchy and present informa-

tion, such as diversity patterns based on taxonomic counts, may be greatly biased by the relatively poor quality of the fossil record (Smith, 1990). The Virgin Limestone spine bed exhibits a preservational style quite typical for echinoids in Early Triassic times (Greenstein, 1990, 1992).

In sharp contrast, the dense sand dollar accumulation of the Miocene Buttonbed Sandstone was deposited well after the radiation of irregular echinoids, which first appeared in Jurassic times. Clypeasteroids have been steadily increasing in diversity since the Paleocene (Smith, 1984). Thus, this echinoid bed was deposited during a prosperous interval within the evolutionary history of irregular echinoids. Clypeasteroids were particularly diverse, accounting for 408 of the 924 species of irregular echinoids recorded from the Miocene (Kier, 1977a).

5.4. Accumulation processes

When reconstructing the accumulation histories of shell beds, it becomes important to recognize the relative importance of biological and sedimentological factors in bed formation. Both biological and physical agents contribute to the accumulation of a fossiliferous deposit; identification of the relative degrees in which these processes influence the bed's deposition is crucial if an accurate understanding of how the bed was formed is to be obtained.

There are many genetic classification schemes based on accumulation processes (Johnson, 1960; Aepler and Rief, 1971; Seilacher and Westphal, 1971; Aigner et al., 1978; Fürsich, 1982; Kidwell, 1982; and others). This paper uses the Kidwell et al. (1986) classification scheme which divides all concentrations into three categories: biogenic, sedimentologic and diagenetic. The three concentration types can be seen as a schematic ternary diagram of the three end members and three intermediate types of accumulations (Fig. 7).

Examination of the stratigraphy, sedimentology and paleontology of the two echinoid beds of this study reveals that the two accumulations were formed by different primary processes. Using the Kidwell et al. (1986) classification, the Buttonbed Sandstone coquina would be classified as a concentration of mixed origin, which combines both biogenic and sedimentologic processes. *V. merriami*

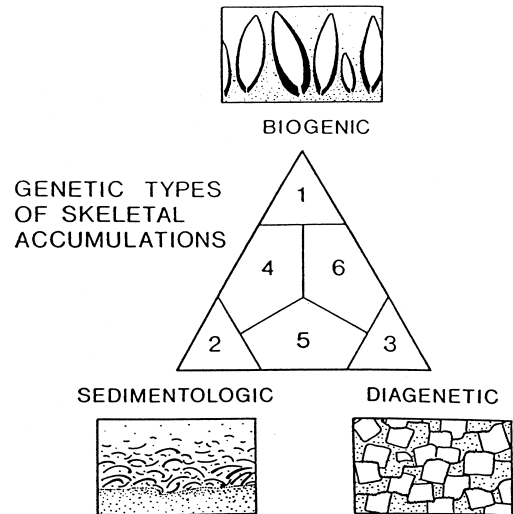


Fig. 7. Schematic ternary diagram of genetic types of shell beds (from Kidwell et al., 1986). A combination of biogenic and overprinting sedimentologic processes, the Buttonbed Sandstone echinoid bed is an accumulation of mixed origins, which is represented by area 4 within the ternary diagram. Although the Virgin Limestone spine bed was certainly affected by both diagenetic and biogenic factors, it is most accurately classified as a sedimentologic accumulation, which is represented by area 2 on the diagram.

populations were abundant within the area, as is evident by their presence in the underlying sandwave lithofacies and their overwhelming abundance in the echinoid bed. Sand dollars are typically gregarious in nature; the masses of *V. merriami* were initially locally deposited as biogenic concentrations. Physical reworking of the area by shallow marine high energy processes greatly overprinted the original biogenic fabric of the bed by winnowing and extensively reworking it. It is a parautochthonous fossil accumulation which was produced by both biogenic and sedimentologic agents.

Unlike the Buttonbed coquina, the Virgin Limestone echinoid bed does not contain fossils found in other surrounding units; the spines present in the echinoid bed are only found within this unit. This is important in understanding the biological control of the accumulation. The low diversity faunal assemblage combined with the high abundance of echinoid spines in the bed suggests that the Virgin Limestone echinoid bed represents a once-thriving community dominated by regular echinoids (which

was reworked and later transported by storm activity). It is these biological controls which define the fossil accumulation. The resulting deposit presents a unique fossil component to the Virgin Limestone member.

It is also important to recognize that diagenetic controls help define the Virgin Limestone spine bed. The partial silicification of the spine material has aided in identifying the echinoid bed; the color contrast of dark brown partially silicified spines and the gray limestone is the primary macroscopic feature of the bed. Without the silicification, the spine bed would take on a very different macroscopic appearance.

Although the spine bed is certainly the product of both biogenic and diagenetic factors, it is not a biogenic or diagenetic concentration. The bed does not directly result from the behavior of shell producers or organisms interacting with the shell material. Nor is its final concentration primarily the product of the diagenetic processes. According to the Kidwell et al. (1986) ternary diagram, this bed would more accurately be classified as a sedimentologic concentration. The limestone unit is a storm deposit which brought regular echinoid material from a shallower area to the more distal portion of the shelf. The fact that there is no evidence of the spines elsewhere in the study area reinforces the conclusion that they are allochthonous in origin. Within the employed classification scheme, the Virgin Limestone echinoid bed should therefore be classified as a sedimentologic concentration.

Comparative analysis of controlling processes along environmental gradients confirms this evaluation of the beds. Kidwell et al. (1986) suggest that nearshore shelfal environments, such as the depositional setting of the Buttonbed coquina, can typically be comprised of concentrations which are primarily sedimentologic in origin or those that have resulted from both sedimentologic and biogenic agents. This depositional environment is dominated by sedimentologic concentrations due to its high energy regime but also includes sedimentologically overprinted biogenic concentrations similar to the Buttonbed Sandstone echinoid bed.

Further offshore, biogenic agents are more controlling of the shell concentrations, as seafloor energy dynamics decrease. Sedimentologic concentra-

tions found in the distal portion of the shelf area are thought to result from rare intense storm events (Kidwell et al., 1986). The Virgin Limestone echinoid bed is most likely an example of this type of concentration, which was preserved in a relatively low energy setting. Bulk deposition of the accumulation during a storm event could explain the lack of bioturbation within the unit, as well as the poorly sorted fossil components and overall lack of consistent orientation of spines within the bed.

6. Conclusions

Through taphonomic, stratigraphic, sedimentologic and petrographic analyses, an understanding of the genesis of the Buttonbed and Virgin Limestone echinoid beds is possible. By examining the conditions of the fossils within the accumulations, as well as other paleoenvironmental indicators within the strata, we are able to reconstruct the depositional history of the beds and determine the processes which produced them. The beds provide examples of how different types of echinoids are preserved in different marine environments. The more resilient sand dollar tests of the Buttonbed echinoid bed proved fairly resistant to high energy neritic processes whereas the taphonomically fragile regular echinoid tests of the Virgin Limestone echinoid bed were destroyed, with only the spines eventually deposited in a relatively deeper marine (distal shelf) setting.

It should be recognized that the echinoid beds presented in this paper are only two of a wide variety of forms that echinoid concentrations can exhibit. Additional deposits must be studied to provide a larger view of what constitutes an echinoid-rich deposit and how these interesting fossil accumulations can form. Also, the relative importance of echinoid concentrations in interpreting the echinoid fossil record should be examined. Consider the hypothesis that much of the diversity of the overall echinoid fossil record may be derived from specimens which occur in shell beds rich in echinoid material. This proposal seems intuitive; paleontologists tend to go where the fossils are. It would seem reasonable that many echinoid taxa may have been described from specimens that came from accumulations which had attracted paleontologists by their high echinoid fossil

content. If a significant proportion of fossil echinoids was first described from the specimens originating in echinoid-rich deposits, then an understanding of the formation of these accumulations is vital in interpreting the nature and biases in the echinoid fossil record.

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