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ECHINODERM TAPHONOMY, TAPHOFACIES, AND LAGERSTÄTTEN

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ABSTRACT—Taphonomic study of echinoderms provides useful information on sedimentary conditions before, during, and after burial. Taphonomic studies of Recent echinoderms indicate that much skeletal disarticulation occurs within a few days after death. However, experiments also indicate that within a short period after death echinoderm carcasses remain rather resistant to disarticulation, and thus may be transported a considerable distance by currents; following periods of a few hours of decay, more delicate portions of echinoderm skeletons are readily disarticulated. Some skeletal modules (e.g., crinoid pluricolumnals) may resist disarticulation for periods of months in quiet- and or cool-water environments. Anoxia promotes intact preservation by excluding scavenging metazoans. Echinoderm ossicles may undergo minor abrasion and/or corrosion if left exposed, and less dense stereom corrodes much more rapidly than dense plates, such as echinoid spines. However, heavily abraded ossicles may indicate prefossilization and reworking.

Various groups of echinoderms (e.g., pelmatozoans, asterozoans, echinoids) have differing propensities for degradation and, therefore, produce different arrays of preserved fossil material primarily depending upon the relative rates of burial, bottom-water oxygenation, and turbulence. Echinoderms may be divided into three groups based upon the relative ease of skeletal disarticulation. Type 1 echinoderms include weakly articulated forms (e.g., asteroids and ophiuroids) that rapidly disintegrate into individual ossicles. Type 2 includes those echinoderms whose bodies contain portions in which are more tightly sutured, as well as portions in which the ossicles are somewhat more delicately bound (e.g., crinoids, regular echinoids). Such echinoderms display more varied taphonomic grades from fully intact to mixtures of isolated ossicles and articulated modules. Type 3 comprises those echinoderms (e.g., irregular echinoids) in which major portions of the skeleton are so resistant to disarticulation that they may be broken across sutures rather than coming apart at plate boundaries.

Comparative taphonomy of particular types of echinoderm skeletal remains leads to recognition of distinctive taphofacies that characterize particular depositional environments. Taphofacies include two types of characteristic modes of fossil preservation: *event taphonomic signatures* and *background taphonomic signatures*. Depending upon normal conditions of environmental energy and rates of sedimentation, the background condition of various types of echinoderms for a given facies may range from articulated, unabraded skeletal modules (in Types 2 and 3) to highly corroded and/or abraded ossicles. Conversely, the occurrence of fully intact fossil echinoderms provides unambiguous evidence of rapid and deep burial of benthic communities. Such well-preserved fossil assemblages can provide a wealth of information regarding the paleobiology of echinoderms, as well as the nature of the depositional events and burial histories.

This paper presents a preliminary classification and characterization of background and event aspects of echinoderm taphofacies for carbonate- (9 taphofacies, including reefs and hardgrounds) and siliciclastic-dominated (5 taphofacies) environments. In each case, we recognize a spectrum of echinoderm taphofacies that coincides with a gradient of environments, ranging from nearshore, high energy shoreface through proximal and distal storm-influenced shelf, to deeper ramp and dysoxic basinal settings. Most taphofacies also feature particular styles of obrution (smothered bottom) Lagerstätten. These range from scattered lenses of articulated fossils in some high energy sandstone and grainstone facies to bedding planes of articulated, pyrite coated specimens in dark shales. We classify and discuss the genesis of these types of Lagerstätten and list typical examples. Finally, we present a simple model that integrates the occurrence of various echinoderm taphofacies with concepts of cyclic and sequence stratigraphy.

INTRODUCTION

TAPHONOMY IS an important aspect of paleoecological analysis, and comprises the study of fossil preservation and related processes that play a role in the incorporation of organic remains into the rock record. Taphonomic research is divisible into two main areas (Seilacher, 1973; Müller 1979): a) biostratinomy, the study of processes that affect organisms from the time of death to final entombment within sediment (e.g., decay, disarticulation, bioerosion), and b) fossil diagenesis, study of physical and chemical processes that occur after burial (e.g., compaction, dissolution, mineralization). Both of these areas provide useful information for the reconstruction of paleoenvironmental conditions, such as sedimentation rate, environmental energy, and sediment/bottom water geochemistry (Brett and Baird, 1986). Taphonomic study of echinoderms can provide useful information on sedimentary conditions before, during, and after burial. Many taphonomic studies of Recent echinoderms indicate that disarticulation and skeletal collapse occurs within hours to days after death, and in some cases, can occur even before death (i.e., autotomy or casting off of arms seen in modern crinoids) (Liddell, 1975; Meyer, 1971). Depending upon the type of skeletal articulation, decay of echinoderm skeletons may yield a variety of skeletal ossicles and modules. The condition of these skeletal components can yield insights into background sedimentation conditions. Conversely, the preservation of completely articulated echinoderms thus requires very rapid to live burial of organisms. Greater lengths of exposure and decay before final burial can be inferred from the progressive collapse and disarticulation of skeletal elements (Figure 1).

The occurrence of intact fossil echinoderms affords dramatic evidence of rapid and deep burial of benthic communities. Such deposits have previously been called "smothered bottom assemblages" or "fossil-Lagerstätten," a term that originally alluded to a "mother lode" (Seilacher et al., 1985). Fossil-Lagerstätten resulting undoubtedly from rapid burial are often referred to as obrution deposits, after "obruere" to smother. Obrution Lagerstätten have been classified into several categories on the basis of associated taphonomic and sedimentologic characteristics (Brett and Seilacher, 1991).

The study of such well-preserved fossil assemblages is critical to our understanding of fossil echinoderms. In fact, most detailed taxonomic and paleoecologic studies have been carried out on fossil assemblages. Obrution Lagerstätten represent taphonomic windows, where benthic communities were preserved essentially *in situ* and removed for the most part from further biotic and abiotic disruption. Careful attention to taphonomy and sedimentology of these deposits can provide a wealth of information regarding the nature of the depositional environment, burial histories of organismal remains and even the paleoecology (paleoautecology) of community members.

Extraordinary assemblages, however, represent but one end-member in a spectrum of preservational grades in echinoderm (and other fossil) assemblages. Less spectacular assemblages of echinoderm skeletal components and ossicles with varying degree of alteration may also provide significant insights into depositional processes and environments.

The major objective of this paper is to place various sorts of echinoderm assemblages into the broader context of environment-related taphofacies. To this end we first consider preservational processes and taphonomic grades in echinoderms, and develop a qualitative classification of echinoderm skeletons based on their propensity to disarticulation. In the second portion of the paper we consider taphofacies of echinoderms and describe a series of generalized taphofacies, including aspects of both typical "background" and event deposits and give environmental interpretations. Finally, we attempt to relate the occurrence of these taphofacies to depositional cycles and sequences to formulate general, predictive models of echinoderm taphofacies, following the lead of Meyer et al. (1989) and Ausich and Sevastopulo (1994). Inevitably, this paper is biased toward examples with which we are most familiar: Paleozoic pelmatozoans; however, we have also attempted to include some other relevant examples.

TAPHONOMIC PROCESSES IN MODERN ECHINODERMS

Recent laboratory and natural experiments have aided greatly in understanding the factors involved in determining the preservational state of echinoderms, such as skeletal architecture and mineral composition, physical working of skeletal material, temperature, oxygen, and decay thresholds (Flessa and Brown, 1983; Meyer and Meyer, 1986; Allison, 1990; Kidwell and Baumiller, 1990). Such studies have recognized the important role of echinoderm skeletal construction in the preservation potential of various echinoid groups (Meyer, 1971; Greenstein, 1991; Allison, 1990; Kidwell and Baumiller, 1990; see Lewis, 1980; Donovan, 1991, for summaries of much of this research).

Under normal aerobic conditions, complete disarticulation of echinoderms into isolated ossicles usually takes place within one to two weeks (Meyer, 1971; Schäfer, 1972; Liddell, 1975; Greenstein, 1991; Kidwell and Baumiller, 1990; Donovan, 1991). Disarticulation of most portions of the arms and cirri of modern comatulid crinoids has been observed to occur within three days after death with only the calyx and short arm segments remaining articulated six days after death (Figure 1; Meyer, 1971; Liddell, 1975; Lewis, 1986). Disarticulation of multielement echinoid skeletons tends to progress with the loss of spine material, decay of peristomial and periproctal membranes and lantern disarticulation, followed by breakup of the corona (Schäfer, 1972; Greenstein, 1991; Kidwell and Baumiller, 1990). The disarticulation of some echinoderms, such as the starfish *Asterias rubens*, may be quickened by the post-mortem stretching and splitting of the organism's skin (particularly affecting the upper portion of the skeleton) by decomposition gases (Lewis, 1980). Field experiments by Sadler and Lewis (1996) confirm the relatively high taphonomic resilience of spatangoid skeletons. Approximately 50% of buried and surface-exposed spatangoid tests remained articulated for up to one year.

Laboratory experiments by Kidwell and Baumiller (1990) and Allison (1990) on the decay and disarticulation of modern regular echinoids show the importance of water temperature and amount of decay in the preservation of echinoid skeletons. Kidwell and Baumiller's research indicates that low water temperatures inhibit organic decomposition more effectively than anoxic conditions (of which the primary role may be in prohibiting scavengers), and that initial decay preceding physical disturbance greatly increases disintegration rates. This study demonstrates that carcasses of freshly killed organisms can endure several hours of jostling in tumbling barrels without significant disarticulation. However, decayed specimens are very rapidly dissociated (Kidwell and Baumiller, 1990).

Recent experimental studies of echinoid taphonomy in natural marine settings (Powell et al., 1995) show that the tests of cidaroids may remain articulated for periods in excess of two years in most modern marine shelf and slope environments. Intact tests also typically show encrusting serpulid tubes and bryozoans after two years exposure on the sea floor.

Physical disturbance, whether biotic or abiotic, greatly increases the disarticulation rate of echinoderms (Meyer and Meyer, 1986; Kidwell and Baumiller, 1990). Study of a fringing reef at Lizard Island, Great Barrier Reef, Australia, points to fish predation as a primary source of both crinoid mortality in the reef area and the concentration of crinoidal debris at the base of the reef (Meyer and Meyer, 1986). Also, predation may account for the scarcity of calyces in the surrounding sediment.

Because of the low density of echinoderm stereom, it is probably less subject to physical abrasion than many other types of shell material; indeed, heavily abraded ossicles may reflect reworking of material in which stereomic pores had been infilled with secondary carbonate (cf., Seilacher, 1973, 1982). However, studies of crinoid ossicles in modern marine environments reveal a loss of surface detail that may be attributed to abrasion and/or corrosion (Meyer and Meyer, 1986). Flessa and Brown (1983) conducted dissolution (acid bath) experiments on irregular echinoid tests as part of a study on the importance of calcium carbonate mineralogy, surface-area/weight ratio of skeletal material and hard part architecture in determining the relative rates and styles of invertebrate skeletal dissolution. Results from the examined echinoids suggest that the relatively high skeletal porosity and high magnesium calcite mineralogy of the specimens contribute to their relatively rapid dissolution rate. In general, the large crystal size of echinoderm plates, especially spines, and their propensity to recrystallize from high to more stable low magnesium calcite favor their long term preservation (Donovan, 1991). Even in rather corrosive, sediment-starved environments echinoderm ossicles may survive longer than most other skeletal carbonates (Seilacher, 1982).

These experimental and observational data provide essential background for the study of comparative taphonomy of fossil echinoderm remains. Salient points include the following (see also Lewis, 1980):

a) Nearly all echinoderms display rapid disarticulation of at least some skeletal parts in normal marine environments. Articulated spines and appendages, such as rays and arms, and the columns of crinoids appear to become detached very readily from tests or thecae.

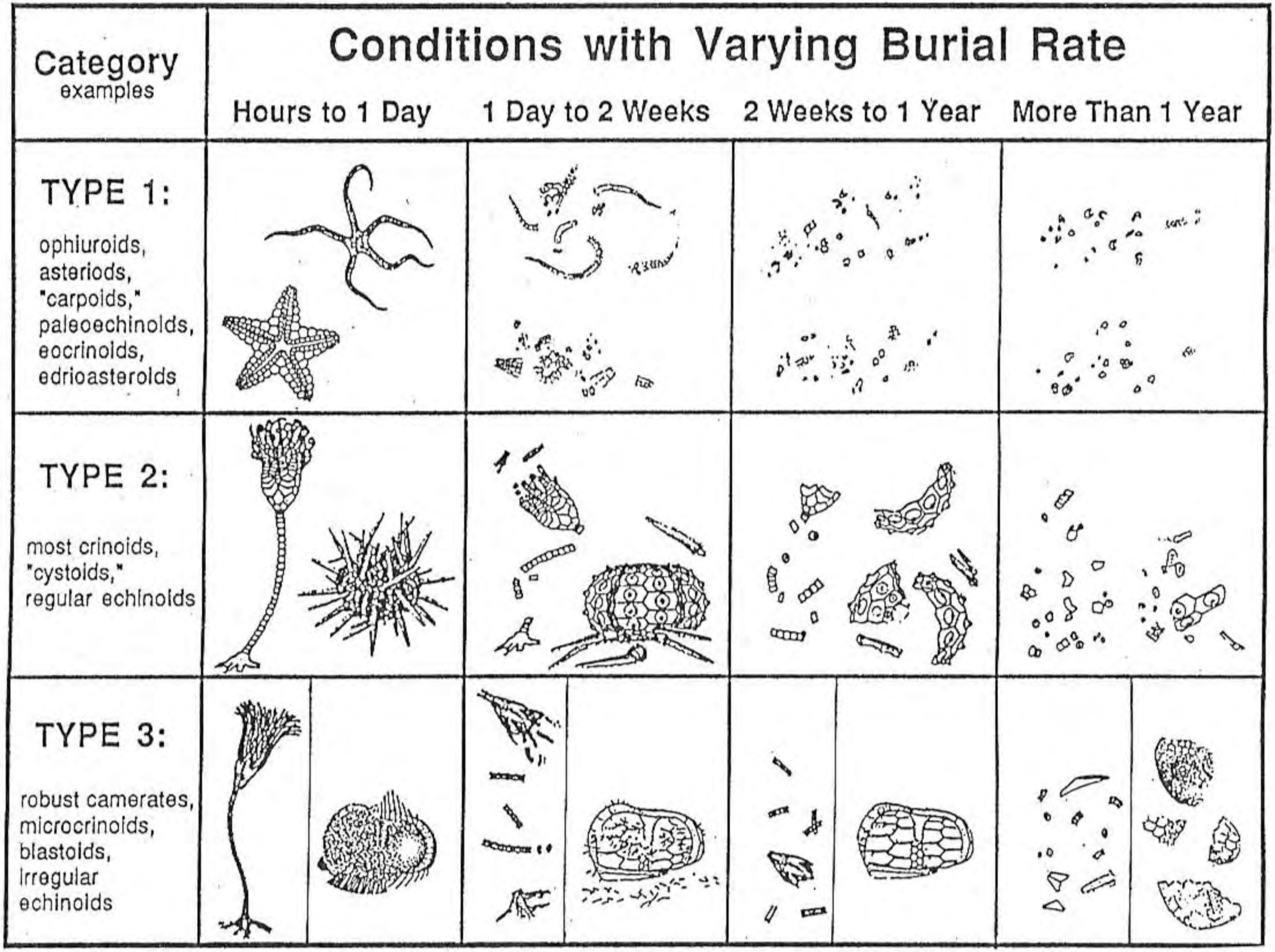


FIGURE *1*—Taphonomic conditions (grades) of three categories of echinoderms (see text for explanation) at varying times of post-mortem exposure.

b) Within a short period after death (typically no more than hours) echinoderm carcasses remain rather resistant to disarticulation, and thus may be transported a considerable distance by currents. Nonetheless, many taphonomic studies of marine offshore environments (Powell et al., 1989; Callender et al., 1992) demonstrate that most skeletons of all sorts tend to accumulate within a few meters of life sites. Following periods of a few hours of decay, more delicate portions of echinoderm skeletons are readily disarticulated by even minor, weak currents or bioturbation.

c) The time required for complete disarticulation of echinoderm skeletons varies substantially depending upon the constructional morphology of the particular skeleton and environmental conditions. Some skeletal modules (e.g., coronas of echinoids, pluricolumnals of crinoids) may resist disarticulation for periods of months in quiet-water environments. This is particularly true of ligamental as opposed to muscular articulations.

d) Cool temperatures and low-energy conditions favor intact preservation and/or association of skeletal ossicles. Both temperature and turbulence will normally decline with increasing water depth such that deeper sites may be expected to show better preservation of intact skeletons, other things being equal.

e) The rate of soft tissue destruction is only slightly lower under anaerobic than aerobic bacterial decay. However, anoxia may promote intact preservation by excluding scavenging metazoans from the burial environment.

f) Echinoderm ossicles may undergo minor abrasion and/or corrosion if left exposed, and less dense stereom corrodes much more rapidly than dense plates, such as echinoid spines. However, heavily abraded examples of originally low density ossicles may indicate prefossilization, early diagenetic infilling of pores and reworking.

TAPHONOMIC GRADES OF FOSSIL ECHINODERMS

Echinoderm fossils display markedly different grades or qualities of skeletal preservation (Figure 1; Table 1). Moreover, distinct groups of echinoderms (e.g., pelmatozoans, asterozoans, echinoids) have distinctive skeletal characteristics and, therefore, produce different arrays of preserved fossil material primarily depending upon the relative rates of burial and other conditions such as bottom water oxygenation and bottom water turbulence. For convenience, we subdivide echinoderms into three groups based upon the relative ease of skeletal disarticulation. Within each group, we consider possible taphonomic grades (*sensu* Brandt, 1989), or modes of preservation within assemblages.

Type 1 echinoderms.—Type 1 consists of very weakly articulated forms, in which the plates are bound together by ligaments or musculature, or are simply loose ossicles embedded within the epidermis of the echinoderm body. Moreover, these echinoderms do not contain modules of more rigidly articulated plates within the skeleton. Thus, it is unlikely that portions of the skeleton will remain articulated for any period of time (i.e., no portion of the skeleton is more rigidly bound together than any other). Such echinoderms would include most asteroids and ophiuroids, many edrioasteroids, and some homalozoans. However, a few loosely skeletonized forms with particularly leathery integuments may remain intact somewhat longer (Lewis, 1980). Also, articulated tests are rarely preserved among the Paleozoic and early post-Paleozoic echinoids because many of them had imbricated plates, which disarticulated rapidly after death.

TABLE *1*—Taphonomic classification of echinoderms on the basis of resistance to disarticulation. Relative abundance of each taphonomic grade is indicated: cc= very common; c= common; rc= moderately common; r= rare; vr= very rare.

CATEGORY/DEFINITION DEFINITIONS	EXAMPLES OF ECHINODERMS	TAPHONOMIC GRADES*			
		A	B	C	D
TYPE 1: ossicles loosely connected, rapidly decay and disarticulate	ophiuroids, "carpoids", asteroids, paleoechinoids, eocrinoids, edrioasteroids	r entire body	vr arms, plates	— plates	c? plates
TYPE 2: skeleton with some, more tightly sutured modules, calyces, thecae, pluricolumnals	most crinoids, "cystoids," regular echinoids	r entire body	c calyx, test	c partial calyx	cc plates
TYPE 3: skeleton with major components rigidly sutured; e.g., tests, thecae	some camerate and microcrinoids, blastoids, irregular echinoids	rc entire body	cc theca test	c theca	r frags

Type 1 echinoderms are the most rarely observed in the fossil record, at least as articulated individuals. Studies of modern forms, particularly asteroids and ophiuroids reveal that disarticulation occurs quite readily, typically within days of death (Meyer, 1971; Schäfer, 1972). Moreover, many of these organisms are mobile and capable of extricating themselves from at least thin burial layers. Hence, they may be able to escape burial events that produce obrution deposits in sessile forms such as pelmatozoans. Therefore, preservation of entire individuals is an extreme rarity associated with live or immediate post-mortem burial.

As a result of the propensity of Type 1 echinoderms to decay and disarticulate, these forms generally display one of two taphonomic grades: either a) (very rare) complete articulated skeletons, sometimes with slight degrees of disarticulation or removal of small portions of rays; or b) completely disarticulated skeletal ossicles, typically unrecognizable portions that are identified in the literature merely as "echinoderm skeletal debris." Comminuted ossicles of Type 1 echinoderms should be abundant in many sediments, but they are rarely identifiable.

Type 2 echinoderms.—This category includes those echinoderms whose bodies contain portions in which the skeletal plates, or ossicles, are more tightly sutured, as well as portions in which the ossicles are somewhat more delicately bound (Figure 1; Table 1). Such echinoderms may display a more varied spectrum of taphonomic grades. Within this group, we would place most pelmatozoan echinoderms, such as crinoids, most blastozoans, eocrinoids, and many regular echinoids. In these echinoderms, incipient decay and partial disarticulation produces skeletal modules, such as tests, dorsal cups or calyces, thecae, and pluricolumnals (segments of articulated columnals or stem joints). Nonetheless, even these portions of the skeleton will disarticulate rather rapidly, provided prolonged periods of exposure on the sea bottom, or attack by scavenging organisms. Type 2 echinoderm skeletons yield a broader spectrum of taphonomic grades, as described in the following paragraphs.

a) Best preserved assemblages consist of entire bodies with articulated appendages, such as echinoid tests with intact spines, or crinoids with intact crowns and articulated columns or stalks. Such assemblages also would be apt to produce entire articulated members of Type 1, such as starfish, and would represent nearly instantaneous burial, either coincident with or immediately following death of the organisms.

b) The next grade of assemblages is characterized by a variety of intact skeletal modules, as well as dissociated ossicles. Such assemblages might, for example, yield whole thecae or dorsal cups of cystoids and crinoids, sometimes with small portions of column attached, in association with pluricolumnals. Arms and brachioles would not remain articulated to crowns, but intact appendages might be found lying loose within the assemblages. It should be noted that, even within Type 2 echinoderms, there is a sliding scale of propensities for disarticulation. For example, Meyer et al. (1989) recognized that certain crinoids, particularly cladid inadunates and flexible crinoids apparently display much more rapid disarticulation, and since these echinoderms also exhibit much smaller dorsal cups or calyces than do most camerate crinoids, they are apt to be less recognizable as modules. The majority of the crown would be represented in such assemblages strictly by disarticulated ossicles, but some portion of the dorsal cup—and in the case of flexibles—the proxistele (the differentiated proximal columnals, which are rigidly adherent to the calyx) might still be preserved. These assemblages would indicate relatively rapid burial of skeletal remains (probably within a few months of death), but certainly not instantaneous burial. A sufficiently long time lag must exist to allow most or all appendages to become detached.

c) The next grade of assemblages would consist mainly of disarticulated ossicles, but with some of the most resistant skeletal modules still preserved intact. Pluricolumnals of pelmatozoans, such as crinoids and cystoids, appear to be among the most resistant of all portions of pelmatozoan skeletons to disarticulation. The interlocking crenulae of columnal facets insure that pluricolumnals remain articulated for prolonged periods of time, even in environments in which there is some degree of turbulence. Studies of pluricolumnals by Baumiller and Ausich (1992) indicate that the columns of many Paleozoic crinoids and the stalks of modern isocrinids have a tendency to fragment into relatively uniformly-spaced increments. Evidently, portions of many crinoid columns have through-going ligaments, which decay slowly and more tightly bind together these portions of the stalks. Conversely, at fairly regular intervals, these through-going ligaments end, and only much more delicate articulations exist. Such a bimodal arrangement of connective tissues within crinoids may suggest a biological function, for example autotomy, in which the crinoid voluntarily casts off a portion of its column under certain conditions, or perhaps, flexibility of the stem. In any event, such modular pluricolumnals are to be expected, and are, indeed, found in many assemblages in which other skeletal modules are lacking, with the exception of the most resistant portions of cups, or calyces, and, of course, pieces of Type 3 organisms. Such assemblages, then, would consist of, mainly, disarticulated single skeletal ossicles with an admixture of pluricolumnals.

d) Assemblages representing truly long-term exposure of Type 2 echinoderms (for periods exceeding several years) would consist exclusively of disarticulated remains. Under such conditions, the only readily-recognizable larger skeletal elements might consist of the more robust spines of echinoids, thick plates of certain pelmatozoans or the holdfasts (rooting structures) of pelmatozoans. Indeed, a special category may be reserved for assemblages that are heavily dominated by intact holdfasts. These assemblages evidently represent the "rooting grounds," or life sites, of pelmatozoans. Surprisingly, however, these root assemblages commonly are not associated with abundant pluricolumnals or thecal plates (e.g., Brett, 1985). This situation apparently reflects the fact that many of these rooting grounds developed in "high-energy" or low-sedimentation environments, such as on hardgrounds and bioherms, or reefs.

Type 3 echinoderms.—Type 3 comprises those echinoderms in which a fairly major portion of the body is rigidly encased in a tightly sutured cup or capsule of plates (Figure 1; Table 1). Such skeletal modules also, of course, include certain of the irregular echinoids, especially the sand dollars, or clypeasteroids. The tests of these echinoids are so resistant to disarticulation that they may be broken across sutures rather than coming apart at plate boundaries. An example of a rapidly buried assemblage of echinoids would be the late Pliocene *Merriamaster* (sand dollar) bed within the San Joaquin Formation of the Kettleman Hills North Dome, California, which exhibits both bare tests and those with spines still attached. Within the bed, many tests are in relatively pristine condition (petal structures and plate boundaries are visible), while others are heavily abraded or corroded. Most specimens display intact tests, but some appear badly crushed yet still distinguishable (see work by Durham, 1978; Dodd et al., 1985).

This category also includes certain pelmatozoan thecae or calyces, such as the rigid calyces of some microcrinoids, dorsal cups of some camerates (e.g., *Eucalyptocrinites*), and especially the thecae of blastoids. These, together with some pluricolumnals of the same organisms, are sufficiently durable that they may even sustain periods of abrasion without becoming disarticulated. Evidently, slight crenulations along sutures, as those between adjacent crinoid columnals, help to hold plates together. Because of their resistance to decay, these echinoderms display fewer taphonomic grades. Hence lower resolution of the dynamics of burial is possible with such echinoderms. The most rapidly buried assemblages would, of course, consist of completely of articulated skeletons with appendages intact, as in the case of types 1 and 2 echinoderms. However, assemblages representing relatively rapid, but not instantaneous, burial may be more difficult to distinguish from those that represent more prolonged exposure on the sea bottom. A relatively rapidly buried assemblage might consist of partially disarticulated pieces of arms and pluricolumnals, as well as some unworn articulated thecae or dorsal cups. Conversely, a long-term, time-averaged assemblage might consist mainly of disarticulated columnal and arm ossicles, with scattered, intact, but abraded and/or bio-encrusted thecae, or dorsal cups. In the case of irregular echinoids, such as sand dollars, it may be very difficult to distinguish between assemblages buried rapidly and those that accumulated more gradually, because the tests are so resistant to disarticulation. However, distinction could be made between those very rare cases in which small spines are preserved intact on the test, indicating very rapid burial, versus those in which tests free of spines are preserved. The latter might also range from complete pristine and unworn tests to those showing high degrees of corrosion and/or abrasion and encrusting by organisms. Beds containing fragments of these echinoids would indicate very prolonged exposure and/or "high-energy" conditions. A good example of such an accumulation is the Miocene Buttonbed sand dollar bed of the Buttonwillow, California area, in which the overall pattern of decreasing abundance of sand dollar tests up section within the coquina is accompanied by an increased abundance of fragments indicating a significant amount of reworking as time progressed in the high-energy shallow-marine environment (Moffat, 1996).

ECHINODERM TAPHOFACIES AND THEIR RELATIONSHIP TO SEDIMENTARY ENVIRONMENTS

General aspects of taphofacies.—Taphofacies are bodies of sedimentary rock or sediment characterized by certain combinations of taphonomic attributes of the contained fossils (Speyer and Brett, 1986). Comparative taphonomy of particular types of skeletal remains leads to recognition that organism skeletons are preserved quite differently in different environments, a phenomenon reported from modern settings (Powell et al., 1989; Callender et al., 1992), and inferred for many fossil assemblages. Taphofacies will display characteristic grades of fossil preservation, such as those described above for echinoderms. However, as noted by Speyer and Brett (1991), taphofacies may display two types of signatures, which have been distinguished as *event taphonomic signatures* and *background taphonomic signatures.*

Background taphonomic signatures.---Background taphonomic signatures are those features of fossil preservation that accrue over long periods of time, during which these remains are variably exposed at the sediment-water interface and are subject to physical, chemical, and biological processing. Preservational attributes reflect environmental processes that prevail during normal day-to-day conditions, as opposed to extraordinary events, such as major storms. Background conditions include aspects of net or average sedimentation rate, environmental turbulence (commonly referred to in terms of "environmental energy;" see Clifton, 1986, for semi-quantitative scales), corrosiveness of bottom waters, bottom water oxygenation, activities of skeletal degrading-organisms, such as endolithic sponges and algae, and rates of bioturbation, and scavenging. These background environmental parameters can be reconstructed, at least qualitatively, on the basis of taphonomic attributes of fossils. Most sedimentary units include some fossils in which preservational features indicate background or long-term environmental processes.

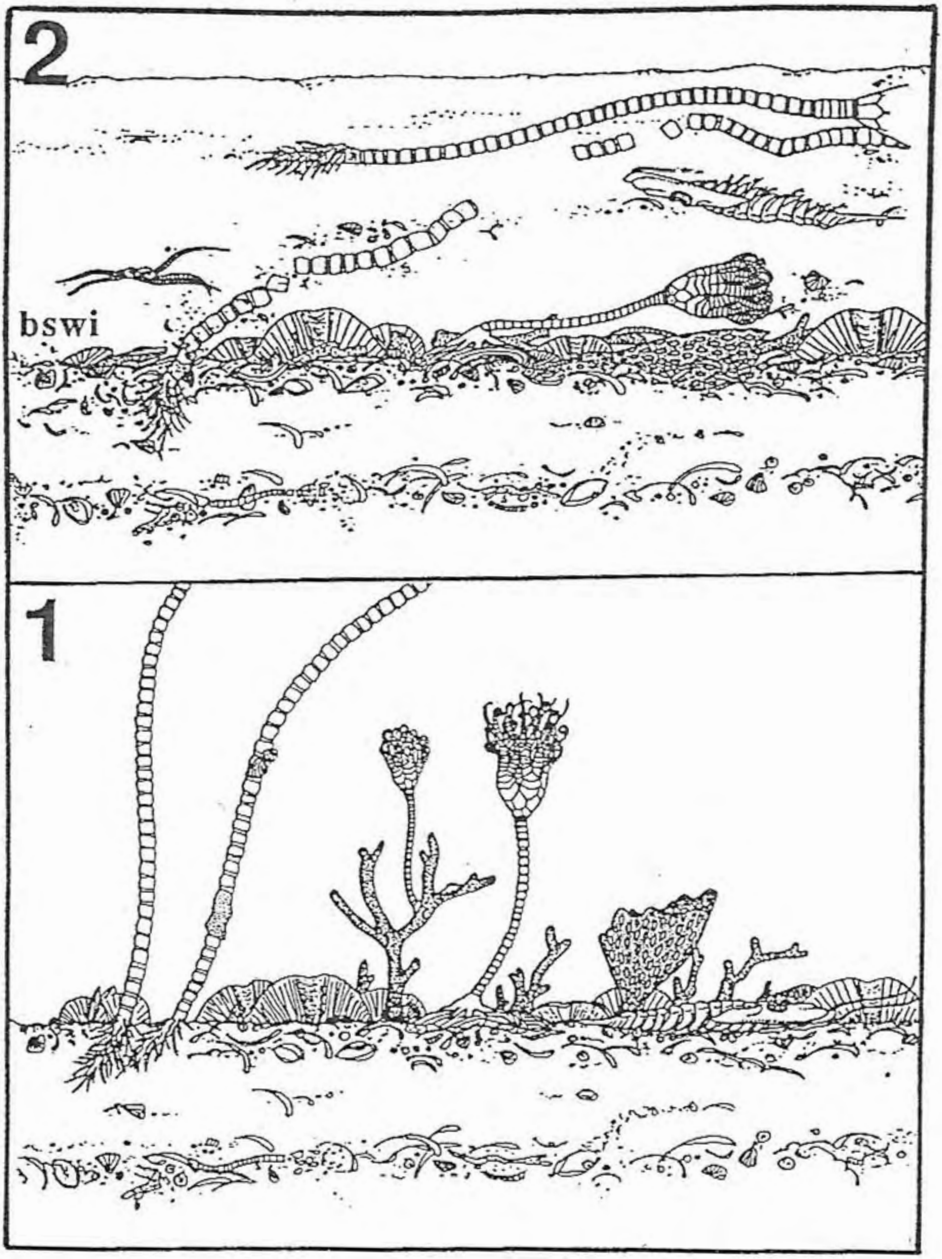
Among the echinoderms, background taphonomic attributes would include the degree of breakage, abrasion, and/or bioerosion and encrustation of skeletal components. Differing grades of skeletal preservation in types 1, 2, and 3 echinoderms have been discussed above. Specific features of echinoderm skeletal preservation also may provide "fingerprints" of certain environments of burial. For example, abraded bioclasts indicate accumulation in high-energy environments, whereas disarticulated, but merely corroded or bio-eroded echinoderm skeletal debris suggests deposition in quiet-water environments. Within each of these taphofacies, there also may exist certain horizons in which extraordinary preservation indicates episodic or pulsed sedimentation within that environment. Such event signatures are considered next.

Taphonomic event signatures: echinoderm Lagerstätten.—Paleontologic event signatures are the record of short-lived, unusual conditions, generally involving rapid sedimentation. Storms, including temperate winter storms and hurricanes, are undoubtedly the most common agent of such event deposits (see Brett and Baird, 1997). Within event beds, the preservation of contained fossils will be radically different from that of fossils accumulated under background conditions. The fragile nature of many echinoderms makes them very sensitive indicators of rates of sediment accumulation and the permanency of burial. It is a reasonable assumption that no echinoderms will show complete articulation under most background rates of sedimentation. Furthermore, if the articulated skeletons of echinoderms of the above-defined types 1 and 2 are fortuitously embedded in sedimentary rocks, they virtually cannot be reworked without disarticulation. Therefore, the occurrence of completely articulated skeletons of crinoids, ophiuroids, or most other echinoderms indicates very rapid and permanent burial. As such, these fossils provide rather unambiguous evidence for very short-lived sedimentary events (Figure 2). Event beds containing remains of echinoderms, particularly those belonging to types 1 and 2 above, are amongst the most readily identified in the fossil record on the basis of biostratinomic features. These beds, which have yielded much of the paleobiological and systematic information on fossil echinoderms, are rare in most sedimentary sections but may occur repeatedly in certain facies, indicating a high episodicity factor. Such echinoderm "mother lodes" or Lagerstätten, are in fact, obrution deposits that represent mass mortality of benthic echinoderms followed by very abrupt burial of remains by a sediment blanket.

Of first-order importance in assessing the nature of obrution beds is to determine whether the organism remains found within them have been buried more or less in place, or have been caught up in a turbid flow and transported some distance prior to deposition of the surrounding sediments. Experimental studies (Kidwell and Baumiller, 1990) have shown that multi-element skeletons of echinoderms may be transported some distance without disarticulation, provided that transport occurs within a few hours of the death of the organisms and prior to decay of connective tissues. Live crinoids display little disarticulation in several hours of tumbling (Baumiller, 1997). Hence, some obrution deposits are strictly allochthonous or transported, whereas others are demonstrably autochthonous, or *in situ*. An important test of these two alternatives has to do with whether or not scattered disarticulated remains of particular species are found in the sediments surrounding the event layers, or whether the species in question are unique to a particular facies and found only in event horizons. Also, the presence of *in situ* holdfasts provides a strong argument for autochthonous occurrences.

Due to the fragile nature of many echinoderms and minute size of their disarticulated ossicles, a particular species may appear to be confined to only one or a few beds, because only at those levels are the animals preserved in such a manner as to be recognizable. The echinoderms may actually have been widespread but their normally comminuted ossicles are not recognized. Brett and Baird (1997) termed such occurrences "taphonomic epiboles," implying that large numbers of particular species of fragile organisms in some beds may simply represent the vagaries of preservation.

The cause of mortality of the echinoderms typically is not known. Under extraordinary circumstances, the animals may, indeed, be buried alive. However, in many cases, there is direct biostratinomic evidence that this is not the case, but rather that sedimentation followed very shortly after mortality and a brief interval of decay. Hence most well-articulated specimens are not complete. Animals may be dislodged from their holdfasts, for example, or a few of the most fragile appendages, such as arms on crinoids, may be missing. Seilacher et al. (1985) contended that echinoderms are particularly subject to death by turbidity. They inferred that echinoderms have an "Achilles' heel" in the form of the water vascular system, which readily becomes fouled and plugged by suspended fine-grained sediment, thereby rendering echinoderms immobile. However, it is known that certain modern vagrant echinoderms are able to work their way out of sediment layers that are deposited rapidly. For example, Schäfer (1972) has documented that some brittle stars and starfish are capable of disinterring themselves from sediment layers up to several centimeters in thickness deposited within a relatively short period of time. That these animals are vagrant and are capable of



RE 2—Taphofacies IIE. Shelly layers in mudstone based on Silurian Rochester Shale showing how an originally tiered community may have been affected by burial. *1*, Hypothetical community with the majority of brachiopods, bryozoans, and some short-stemmed echinoderms living several centimeters above or directly on the substrate. Higher tiers are dominated by long-stemmed pelmatozoans. *2*, Communities may be buried *in situ*; the taphonomy of the smothered fossil assemblage reflects the original tier structure. Those preserved directly on the buried sediment-water interface (bswi) are low level forms while higher tier or mobile forms (intermediate- and long-stemmed pelmatozoans, stelleroids, and trilobites) are buried up to five centimeters above the bswi in "barren" mudstone.

extricating themselves from sediment layers may contribute to the overall rarity of echinoderm lagerstätten containing such forms as starfish and ophiuroids. Sessile organisms, particularly those close to the sediment-water interface, such as edrioasteroids, are much more subject to mortality by direct burial. Nonetheless, these forms are rarely seen as articulated individuals, which indicate the overall rarity of sediment-blanketing events that are sufficiently rapid to prevent the disarticulation.

Another important factor is that echinoderms of various types that live at different levels relative to the sediment-water interface of the sea floor not only may have differing responses to sea floor disturbances, such as distal storm currents and associated perturbations in water mass conditions, but also the remains of these animals may be embedded at different levels relative to the original sediment-water interface (Figure 2). Any obrution layer fundamentally has at least three components that may each show a taphonomic response: a) the sediment mass below the sediment-water interface, which may contain entombed remains of burrowing organisms, rarely including echinoderms, such as ophiuroids, b) the buried sediment-water interface displaying the remains of sedentary epibenthic forms, such as rooted pelmatozoans and edrioasteroids, and c) the burial sediment itself, constituting the layer of newly deposited sediment, which accumulated rapidly on the old sediment-water interface. Each of these zones has distinctive taphonomic attributes. Moreover, various members of tiered (multi-level) benthic communities will tend to be entombed at different characteristic levels relative to the sediment-water interface (Figure 2). Thus, long-stalked crinoids may collapse after a certain amount of burial sediment has accumulated. Such remains are most typically distributed in otherwise barren mudstone burial layers; remains of other organisms such as ophiuroids that were foiled in attempting to burrow out of the sediment layer may also be found in unusual attitudes in the otherwise barren burial sediments. Longer-stemmed crinoids, which extend 10–100 cm or more above the sea floor, may be more readily uprooted and removed from their original burial sites and redeposited as parautochthonous, or even allochthonous (transported) assemblages.

One further important attribute that helps to characterize the taphonomic history of a particular sedimentary unit is the frequency, or number of occurrences, of event beds, which qualitatively has been termed "episodicity" (Brett and Baird, 1986; Speyer and Brett, 1986, 1988), and might be quantified in terms of numbers of discrete events preserved per unit thickness.

All well-preserved echinoderm Lagerstätten could be assigned to a generalized "obrution bed taphofacies." However, detailed observations of the sedimentology and taphonomy of associated, non-articulated fossils suggest that these beds are generated under widely different sedimentary regimes, and are parts of otherwise distinctive taphofacies. Events of sedimentation may occur in a wide array of settings, from relatively shallow to deep, from high energy to low energy, each of which will yield a taphonomic signature of well-preserved fossils. Brett and Seilacher (1991) produced a preliminary classification of obrution deposits, many of which contain abundant echinoderms. This classification roughly follows a spectrum of event-bed proximality, as described for storm layers (Aigner, 1985). That is, certain types of rapid-burial beds with key characteristics occur in high-energy nearshore, or grainstone deposits, whereas others are found at tops of storm beds in somewhat more distal settings; still others are found as parts of mudstone in deep-water settings; and finally, others may represent allochthonous turbidites in which echinoderms are entrained and buried after transport. In this paper, we do not treat obrution deposits as a taphofacies in their own right, but attempt to integrate the genetic classification of Brett and Seilacher (1991) with information on background taphonomic or preservational attributes of echinoderms.

CLASSIFICATION OF GENERALIZED ECHINODERM TAPHOFACIES

In the following sections, we discuss and interpret several generalized recurring taphofacies of echinoderm-dominated assemblages. They are organized along a roughly proximal-nearshore to offshore facies spectrum, beginning with relatively coarse-grained, low-sedimentation and high-energy, turbulent environments and their record, and moving (with higher numbers) generally more offshore to finer grained accumulations. The taphofacies have been numbered in two parallel series, each of which represents an approximately proximal to distal spectrum. The "I" series comprises taphofacies characteristic of carbonate-dominated environments with low terrigenous input, whereas the "II" series reflect taphofacies of siliciclastic-dominated settings; within each series letter designations represent a spectrum of proximality, with A representing the highest energy, generally most proximal settings. Tables 2 and 3 summarize sedimentological and taphonomic characteristics and list typical examples of each taphofacies. The following sections consider both background and event taphonomic characteristics of each taphofacies and discuss inferred environmental conditions responsible for their generation. A single type of taphofacies may characterize two very distinct environments (e.g., IE). In such cases, the stratigraphic context of the sample is critical in inferring paleoenvironment. Note also that no counterpart of the reefal taphofacies (IB) is recognized in siliciclastic-dominated settings, hence, no IIB category has been proposed.

CARBONATE-DOMINATED TAPHOFACIES

The "I" series of taphofacies is developed in settings with low siliciclastic input (e.g., carbonate shelf, reef, ramp and basin). In actuality, many of these also occur in areas of mixed carbonates and siliciclastics. Thus, there is no hard and fast division between this suite of taphofacies and those of the siliciclastic suite. The division is simply one of convenience.

Taphofacies IA: skeletal shoals.—This taphofacies is represented by relatively thin, and commonly very widespread blanket-like deposits of echinoderm skeletal grainstone and packstone deposits, as well as local and lenticular buildups of echinoderm skeletal debris. These deposits may feature erosional scours, internal truncations, and hummocky or trough cross-stratification of skeletal debris. Skeletal debris typically is sorted to some degree and commonly occurs as amalgamated, vaguely graded beds.

Crinoidal grainstones, common in many Paleozoic to early Mesozoic sedimentary successions, such as the Mississippian Burlington and Banff–Rundle Formations, provide excellent examples (Ausich, 1997). Among echinoids, spine beds of the sorts described by Moffat (1996) provide a probable analog.

Background taphonomic attributes of echinoderms of these accumulations include nearly complete disarticulation of types 1 and 2 echinoderms. Some intact skeletal modules or groups of articulated plates may also occur, but they tend to be rare and scattered. These belong primarily to Type 3, those with very tightly sutured calyces (e.g., camerate crinoids), thecae, or tests. For example, in Paleozoic sediments, intact but sometimes abraded thecae of blastoids, or of small, compact camerate crinoids may occur throughout these intervals, rarely aggregated in local small pockets. Holdfasts of pelmatozoans tend to be rare in these assemblages, and when present, are typically reworked rather than *in situ* (e.g., overturned specimens, evidence for abrasion or overgrowth of sutures by epibionts, etc.). Pelmatozoan pluricolumnals and the rigid tests and spines of certain echinoids may also occur abundantly within these sediments. Individual echinoderm ossicles, such as crinoid columnals, may display abraded exteriors and/or pressure solution. The latter effect, produced during deep burial diagenesis, may, unfortunately, obscure certain aspects of the primary taphonomic signature.

Some skeletal modules, such as resistant calyces, thecae, and tests of Type 2 and especially Type 3 echinoderms occur scattered within skeletal grainstones. Event deposits within this facies are less common and typically very lenticular. However, occasional lenses of completely articulated crinoids or other fragile echinoderms may occur; these were referred to as "Hauptrogenstein" type obrution deposits (Meyer, 1988; Brett and Seilacher, 1991). However, a more familiar and typical example is the Mississippian Burlington Limestone of the Mississippi Valley. This widespread skeletal grainstone has yielded countless well preserved calyces of camerate crinoids, blastoid thecae and more rarely completely articulated fossils.

Much of the Paleozoic and early post-Paleozoic echinoid fossil record is based on such accumulations comprised of spines alone. For example, the vast majority of Triassic type species of Cidaridae, the only family traditionally thought to have survived the Permian–Triassic mass extinction, is described from spines (Greenstein, 1992).

Echinoderm grainstones typify shallow, offshore carbonate shoals. Micritization of grains suggests accumulation of skeletal debris in the photic zone, and abrasion and size sorting indicate repeated reworking in turbulent environments near wave base.

Not surprisingly, relatively few skeletal remains are preserved intact, but occasional storms abruptly reworked layers of debris and permanently buried some echinoderm skeletons. Much of the skeletal debris consists of locally transported sand- to gravel-sized ossicles. The source of this debris is either *in situ* deposition or from nearby colonization sites. In some instances, local patches of stabilized muddy sediment yield abundant holdfasts of pelmatozoans. These lenses evidently represent rooting grounds, the life sites of at least some of the echinoderms whose skeletal remains were transported shoreward, and reworked primarily by fair-weather wave action (Figures 3, 6). Gravel- and sand-sized ossicles were concentrated near wave base to form skeletal shoals. It is probable that more vagile echinoderms, such as starfish, echinoids and crinoids with flexible cirriferous holdfasts, were able to colonize the shoals directly and upon death, contributed further debris. Messing (1997) has noted that cirriferous stalked crinoids may even shed portions of their columns, contributing skeletal debris while living. We anticipate that rapid burial of carcasses of echinoderms by shifting skeletal sediment may have occurred frequently. However, subsequent reworking and destruction of these buried assemblages also would occur almost as frequently. The rare Burlington (or Hauptrogenstein) type deposits evidently represent mortality and burial events that fortuitously escaped later reworking.

Taphofacies IA': shoal top Hardground.—These are surfaces that occur within or, commonly, at the upper contacts of massive skeletal grainstone deposits (Table 2). They are planar to undulating, sharp, darkly stained (phosphatic, manganese) mineralized surfaces, or undercut pockets and are sharply overlain by additional layers of skeletal debris, or calcareous shales. These hardgrounds possess borings and fossils of encrusting organisms. In general, attached fossils are incomplete (e.g., pelmatozoan holdfasts) and they may be abraded, especially where the hardground is overlain by

TABLE 2—Summary table of echinoderm taphofacies in carbonate-dominated facies. See end of table for references to Lagerstätten examples (superscripted numbers).

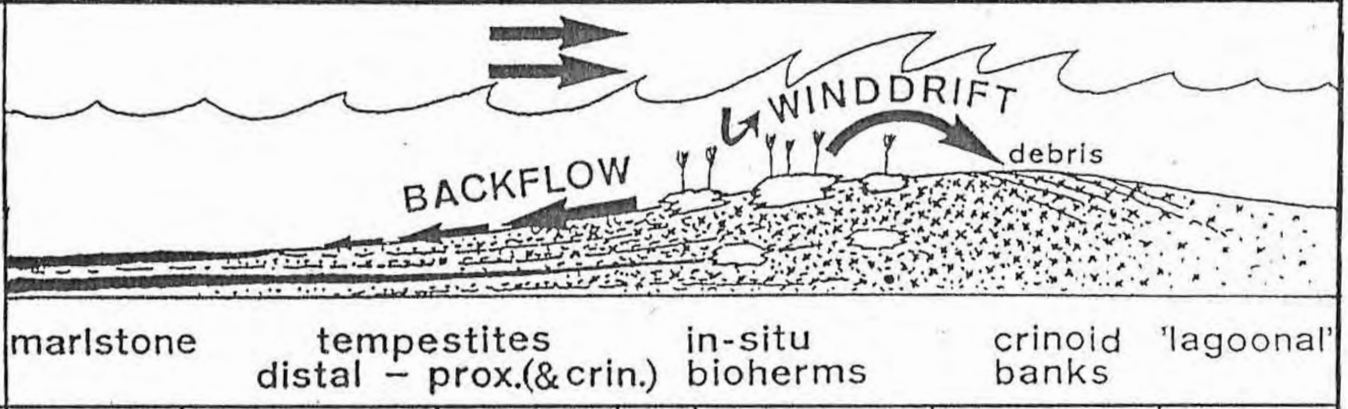
TAPHOFACIES/ INFERRED ENVIRONMENT	LITHIC /TAPHONOMIC CHARACTERISTICS	LAGERSTÄTTEN TYPE AND EXAMPLES
IE'—LAGOON soft, carbonate mud to silt substrate; restricted, shallow water above wave base	thin-bedded, platy, calcisiltites, minor ossicles, articulated, current-aligned skeletons	LITCHFIELD TYPE Dev.: Manlius/ Coeymans Ls. Litchfield, NY[15]
IA—CARBONATE SHOAL loose, skeletal sand-gravel substrate; shallow, high energy, at or near normal wave base	massive skeletal, pack/grainstone, cross-strat. mostly disarticulated, some fragmentation, corrosion	BURLINGTON TYPE Sil.: Gasport Fm., NY, Ont.[6] Miss.: Burlington Ls., IA[30] Fort Payne, KY[41] Jur.: Hauptrogenstein, Switzerland[39]
IA'—SHOAL TOP HARDGROUND hard substrate, shallow, high energy, at or near normal wave base	hummocky to planar, corroded, bored, and encrusted hardground at top of massive skeletal ls., rare articulated/ intact pelmatozoan holdfasts	MUSCHELKALK TYPE Sil.: Laurel Ls. (top), IN[21] Dev.: Shell Rock, IA[28] Trias.: Muschelkalk, Germany[20]
IB—BIOHERM/REEF firm mud-skeletal substrate (core); loose skeletal sand, gravel (flanks); moderate to high energy; slightly below wave base	a) massive micritic boundstone with *in situ* holdfasts, minor debris-filled pockets b) clinoform flank beds; disarticulated and partially articulated skeletons; grading	RACINE TYPE Sil.: Racine Dol. WI[37, 56] Hopkinton Dol., IA[14] Hogklint Reefs, Gotl.[15] Miss.: Waulsort buildups, Ft. Payne, KY[2, 41]
IC—STORM DOMINATED SHELF/ SHOAL MARGIN/ RAMP soft mud to skeletal gravel; low to moderate energy; below normal but above storm wave base	thin-medium bedded, shelly wacke/grainstone interbedded with calcareous shale, mainly disarticulated ossicles;but abundant articulated fossils may occur on upper (rarely lower)bedding planes.	CINCINNATIAN TYPE Ord.: Cinn., OH[40, 45] Lebanon Ls., TN Miss.: Hampton Ls., IA Hook Head Ls. (Supra-dol. beds), Ireland[3] Monteagle Fm., AL[24] Penn.: Stanton Ls., KS[23] Trias.: Muschelkalk Ls., Germany[20, 35]
IC'—SHOAL MARGIN HARDGROUND hard substrate, low to moderate energy; above storm wave base	bored, encrusted minor hardgrounds on tops of thin, skeletal limestones; some corrosion, articulated intact pelmatozoans	GMEUND TYPE Ord.: Bobcaygeon Ls., Kirkfield, Ont.[7,51] Lebanon Ls., TN[18] Jur.: Gmeund Ls., Germany[43]

ID—DEEPER, STORM INFLUENCED SHELF soft substrate; low energy; near lower limit of storm wave base; minor influence of gradient currents	thin- to medium-bedded tabular to nodular, sometimes cherty, micritic limestone(wackestone) or chalk; bioturbated; skeletons mainly as disarticulated ossicles, *in situ* collapse of skeletons, articulated echinoderms on bedding planes	CHALKY LS. TYPE Ord.: Platteville Ls., IA[29] Girardeau Ls., MO[9] Dev.: Onondaga, NY[15] Trias.: Virgin Ls. (echinoid bed), CA[27] Cret.: "The Chalk" (echinoid beds), Eng.[26]
IE—DISTAL SHELF/ RAMP soft, carbonate mud to silt substrate; low energy; below storm wave base, but affected by gradient and/or turbidity currents	thin-bedded, tabular, graded, skeletal lags to laminated calcisiltite-calcilutite, shale; minor ossicle lags at bases; articulated, rarely aligned skeletons on bed bases, tops, rarely, internally; may be allochthonous	RUST QUARRY TYPE Camb.: Spence, Wheeler Sh. (Eocrinoid beds), UT[50] Ord.: Trenton Ls. 'Walcott-Rust quarry,' NY[59] Carb.: Hook Head Ls., ('*Chonetes*' beds), Ire.[3]
IF—DYSOXIC/ ANOXIC BASIN soft, mud substrate, low energy; restricted, dysoxic to anoxic basin or lagoon; may have elevated salinity	platy, laminated, calcilutite (micrite), may be shaley bituminous dolostone, much material articulated, but typically decalcified; may be allochthonous	SOLNHOFEN TYPE Sil.: Mississinewa "Shale" IN[33]; Eramosa Dol., Ont.[36, 56] Jur.: Solnhofen Ls., Germany[22, 47]

REFERENCES FOR TABLES 2 AND 3

0–P. A. Allison (personal communication, 1997); 1–Ausich (1997); 2–Ausich and Meyer (1990); 3–Ausich and Sevastopulo (1994); 4–Ausich et al. (1979); 5–Bishop (1975); 6–Brett (1985); 7–Brett and Liddell (1978); 8–Brett and Seilacher (1991); 9–Brower (1974); 10–Brower (1995); 11–Brower and Veinus (1978); 12–Feldman (1989); 13–Franzén (1982); 14–Frest et al. (in press); 15–Goldring (1923); 16–Goldring (1978); Goldring and Langenstrassen (1979); 17–Goldring and Stephenson (1972); 18–Guensburg (1984); 19–Guensburg (1992); 20–Hagdorn (1985); 21–Halleck (1973); 22–Hemleben and Swinburne (1991); 23–Holterhoff (1997); 24–Horowitz and Waters (1972); 25–Kammer (1982); 26–Kennedy (1978); 27–Kier (1977b); 28–Koch and Strimple (1968); 29–Kolata (1986); 30–Lane (1969); 31–Lane (1963, 1973); 32–Lane and Ausich (1995); 33–Lehmann and Pope (1989); 34–Liddell and Brett (1982); 35–Linck (1965); 36–LoDuca and Brett (1997); 37–Lowenstam (1957); 38–McIntosh (1978); 39–Meyer (1988); 40–Meyer (1990); 41–Meyer et al. (1989); 42–Roeser (1986); 43–Rosenkranz (1971); 44–Sass and Chondrate (1985); 45–Schumacher and Ausich (1983); 46–Seilacher (1968); 47–Seilacher et al. (1985); 48–Sellwood (1978); 49–Simms (1986); 50–Springer (1911); 51–Springer (1926); 52–Sprinkle (1973); 53–Sprinkle (1982); 54–Sprinkle and Gutschick (1967); 55–Taylor and Brett (1996); 56–Tetreault (1995); 57–Watkins (1991, 1993); 58–Wells (1941); 59–Whiteley et al. (1993).

Carbonate Dominated Settings



Tapho -facies	IE	ID	IC	IB	IA	IE'
Deposit. Setting	Distal Shelf/Ramp	Deeper Storm-Infl. Shelf	Storm-Dominated Carbonate Shelf	Reef and Reef Flanks	Skeletal Shoals	Lagoonal
Dominant Lithology/ Bed Geometry	thin-bedded, tabular calcisiltite-calcilutite, shale	thin- to med.-bedded, tabular to nodular, commonly cherty, micritic limestone/chalk	thin- to medium-bedded shelly wacke- to grainstone interbedded with calcareous shale; hardgrounds may be present (IC')	a) massive micritic boundstone (reef rock); b) clinoform flank beds	massive skeletal pack-grainstone; hardgrounds may be present (IA')	thin-bedded, platy calcisiltites
Prim. Sedim. Struct.	subtly laminated units; very minor skeletal lags at bed base	bioturbated; very thin skeletal hash beds	sharp basal beds with tool marks; normal grading; small scale hummocky cross stratification (HCS)	grading; fissures filled with debris; firmgrounds; in bioherms, minor burrow mottling, vugs	planar and trough cross-stratification (incl. herringbone); scour and fill; amalgamated graded bedding	minor graded bedding; planar to wavy laminated
Dominant Taph. Features	ossicle lags at bed bases; art., rarely aligned skeletons on bed bases, tops, or rarely, internally	mainly disarticulated ossicles; in situ collapse of skeletons; articulated echinoderms on scattered bedding planes	mainly disarticulated ossicles; abundant articulated fossils on upper (rarely lower) bedding planes	in situ holdfasts and minor debris-filled pockets in reef rock; disarticulated and partially articulated skeletons in flanks	mostly disarticulated; some fragmentation, abrasion and corrosion of ossicles (high diversity)	minor ossicles; art. current aligned skeletons (low diversity)

FIGURE 3—Summary diagram of echinoderm taphofacies and associated stratigraphic, sedimentologic, and taphonomic characteristics for carbonate environments. Environmental schematic modified from Aigner (1985).

coarse skeletal debris. However, other examples, such as some hardgrounds in the Triassic upper Muschelkalk Limestone (Hagdorn, 1985), display intact, articulated fossils such as crinoids cemented by discoidal holdfasts. Paleozoic hardgrounds may show cystoids or edrioasteroids (Koch and Strimple, 1968; Table 1). They display many features in common with Type IB' taphofacies, discussed below, but generally represent more profound discontinuities, such as maximum flooding surfaces. A change to lower energy conditions coupled with sediment starvation in these cases permitted stabilization and cementation of skeletal shoal sediments. Although many generations of encrusters on the hardgrounds may have been completely lost by export or dissolution of skeletal ossicles. However, in rare cases a final pulse of sediment buried the surface very rapidly, preserving the last community in detail.

Taphofacies IB (reefal taphofacies).—Echinoderm fossils may occur very abundantly in association with fossil reefs and bioherms (Figures 3, 6; Table 2). This really is a composite of two closely related taphofacies types: those of reef cores (IBa), and those of flank beds (IBb). The lithology of the reef-rock itself is typically massive micritic boundstone with variable content of framebuilding corals, stromatoporoids, bryozoans, or algae. In many cases, the bioherms themselves may be largely free of disarticulated skeletal debris. However, holdfasts of pelmatozoans may be very abundant. Holdfasts include varied radices ("roots" with branching radicles) and creeping holdfasts or stolons and runners (Franzén, 1977; Brett, 1985). These holdfasts are directly anchored within the boundstone matrix of the bioherm or cemented to skeletal objects such as bryozoans or corals. In some bioherms local depressions or "pockets" may accumulate skeletal debris, including pluricolumnals of pelmatozoans and rarely, articulated thecae or calyces. An excellent example of the latter is provided by Ordovician reefs of Olan, which display "pockets" replete with spar-filled thecae of the diploporitan cystoid *Echinosphaerites* ("crystal apples;" see Bather, 1918).

The margins of bioherms commonly display dipping flank deposits of skeletal debris. Skeletal grainstones and rudstones predominate. These flank deposits have many of the attributes of taphofacies IA, although the frequency of articulated specimens may be somewhat higher. Flanks of mid-western Silurian reefs, for example, yield abundant mostly armless calyces and pluricolumnals of camerate crinoids and rhombiferans. Flank beds may display crude grading and sometimes alignment of skeletal debris. A remarkable observation is the occurrence of numerous vertically oriented crinoid columns in Silurian reef flank beds from Illinois (Donovan et al., 1997).

The abundance of pelmatozoan holdfasts in some better preserved (non-dolomitized) bioherms and reefs proves that these stable elevated areas provided "rooting grounds" for these animals (Brett, 1985). The absence of other skeletal debris from these structures (except in local pockets) further indicates that they were typically swept by waves or currents that removed any accumulating loose material. Indeed, the great abundance of pelmatozoan ossicles (other than holdfasts) in flank beds indicates that debris was washed off from the exposed, elevated bioherm surfaces and accumulated in clinoform debris beds. The relatively well articulated character of much of the pelmatozoan debris, as well as grading of flank beds, and the rare upright crinoid stems suggest very rapid emplacement of skeletal sediment, probably during major storm washing of the reefs. Articulated modules of types 1 and 2 echinoderms are common, but complete bodies are rare. This observation may indicate that most of the living echinoderms were sufficiently well-anchored that they were not torn off and redeposited and/or that the turbulence associated with burial was severe enough to physically tear carcasses/live animals apart. In any case, much of the transport of debris was quite local.

Taphofacies IC: storm-dominated carbonate shelf/proximal ramp.—This taphofacies is recorded in heterolithic, interbedded mudrock and thin-bedded, skeletal pack- and grainstones interbedded with calcareous shales. Bioclasts include varied echinoderms, brachiopod and mollusc shells, bryozoans, and corals (Figures 3, 6; Table 2). Echinoderms occur primarily as disarticulated to fragmented, and rarely abraded, skeletal ossicles within the pack- and grainstone beds. Skeletal debris may display normal size grading within beds, with large shells and echinoderm skeletal modules, such as robust crinoid pluricolumnals, portions of thecae or plates and spines of crinoids and echinoids, near the bases of the beds. Sediment within the beds may fine upward into planar-laminated to small scale hummocky cross-stratified, sand- or silt-sized skeletal debris and pellets. Bed bases commonly are sharp and tops may display distinctive post-event burrowing (Pemberton and MacEachern, 1997).

Complete echinoderm skeletons may occur rarely on the bases of, or within the pack- or grainstone layers. Also, as in taphofacies IIC, "logjams" of parallel aligned crinoid columns may occur in some beds. These occurrences provide evidence for at least local transport and rapid redeposition of skeletons; the well-preserved echinoderms evidently represent carcasses that were caught up in turbulence events and buried rapidly and permanently by skeletal debris.

More commonly, well-preserved remains are found along the upper surfaces of the limestone beds and are covered by a matrix of calcareous shale (or carbonate mudstone). Many excellent echinoderm obrution beds represent this taphofacies, such as the exquisitely preserved crinoids and blastoids of the Mississippian Hook Head Formation ("Supra-dolomite beds," Ausich and Sevastopulo, 1994; Figure 7) and the Monteagle Limestone in near Huntsville, Alabama (Horowitz and Waters, 1972; see Table 1).

Sessile forms, such as crinoids or edrioasteroids, may be attached directly to the skeletons of other organisms. Excellent examples of this type of occurrence are provided by Upper Ordovician edrioasteroid beds in the Cincinnati Arch area, described by Meyer (1990); here the edrioasteroids grew on a pavement of convex upward strophomenid brachiopod shells on the tops of limestone beds. Such "Cincinnatian" type Lagerstätten evidently represent remains of organisms that colonized tops of skeletal debris layers after the latter became stabilized. The edrioasteroids ultimately were decimated and buried by an influx of mud. Such assemblages are clearly related to hardground Lagerstätten (Taphofacies IC'; see below) and, like the latter, indicate minor periods of exposure and colonization of shelly debris on the seafloor, punctuated by permanent mud burial. Presumably, many such assemblages were buried only to be later reworked.

In many of these heterolithic limestone-shale successions, the shelly carbonates represent winnowed and multiply-reworked bioclasts; the skeletal debris accumulated gradually under (slow) background sedimentation conditions. Features such as hummocky cross-stratification, sharply scoured bases, and/or rippled tops in these skeletal beds indicate processing by one or more major storm events (Aigner, 1985). Taphonomic evidence proves that the intervening mud(stone) layers commonly may not represent "background" conditions, but rather pulses of redeposited fine-grained sediment redeposited from distal gradient currents following less severe storms.

Conditions conducive to the development of these taphofacies exist in environments close to average storm wave base, such as outer margins of carbonate shoals. In such areas the bottom was episodically stirred by waves/currents strong enough to resuspend sand- and gravel-sized skeletal debris in an otherwise quiet, low-energy setting in which skeletal debris of resident organisms simply accumulated.

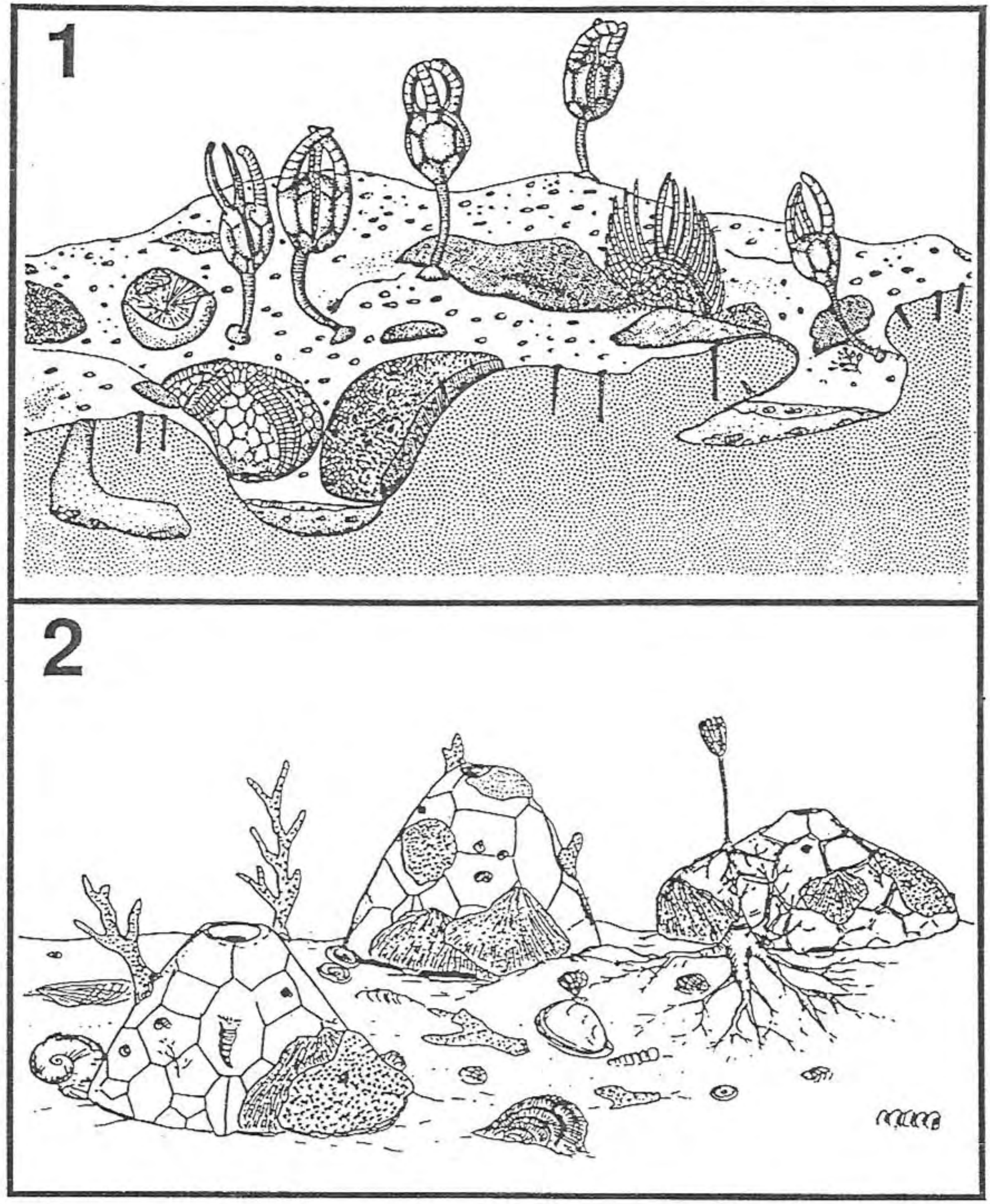


FIGURE *4*—Hard substrates and echinoderms. *1*, Community of small hybocrinids (*Hybocystites*) edrioasteroids (*Edriophus*), and paracrinoids attached to a hardground from the Middle Ordovician Bobcaygeon Limestone at Kirkfield, Ontario; from Brett and Liddell (1978); 2, Calyces of *Eucalyptocrinites* that served as hard substrate "islands" for encrusting bryozoan assemblages on a muddy sea floor; Silurian (Wenlockian) Waldron Shale near Nashville, Tennessee; from Liddell and Brett (1982).

Taphofacies IC': shoal margin/shallow shelf hardgrounds.—This taphofacies occurs in association with taphofacies IC where firm- and hardgrounds occur at the tops of carbonate beds due to syn-sedimentary lithification of carbonate sediment (Figure 4-1; Table 1). In such instances, sharply defined burrow walls and/or the presence of boring and encrusting organisms on the tops of limestone or concretionary beds indicate early cementation to form firm- or hardgrounds. Under conditions of slow sediment burial, pelmatozoans may be represented primarily by discoidal or dendritic holdfasts that remain cemented directly to the hardground. Other portions of echinoderm skeletons typically are represented only by scattered debris on the hardground surface or may be absent.

More rarely, complete bodies of echinoderms, such as edrioasteroids and/or short-stemmed crinoids, may occur adhering to these surfaces. They typically are overlain sharply by sparsely fossiliferous mudrock. However, the latter, in some instances, also may contain exquisitely preserved remains of crinoids, asteroids, or echinoids that were directly attached to the underlying shelly debris or hardground.

Such exceptional occurrences represent the so-called "Gmuend-type Lagerstätten" of Brett and Seilacher (1991). In this example described by Rosenkranz (1971), a Jurassic nodular hardground apparently representing a transgressive lag was overlain by mudstone containing exquisitely preserved crinoids, starfish, and echinoids. Other good examples of this taphofacies include Middle Ordovician hardgrounds from Ontario with intact edrioasteroids, hybocrinids, paracrinoids and other echinoderms (Brett and Liddell, 1978; Brett and Brookfield, 1984; Figure 4-1). Many Cambrian and early Ordovician hardgrounds were developed on intraclastic (flat pebble) conglomerates, which constituted an important habitat for early attached echinoderms (see Sprinkle and Guensburg, 1995).

Hardgrounds represent diastems, or breaks in sedimentation that were followed by abrupt pulses of fine-grained sedimentation. As such, these are similar to the Cincinnatian type Lagerstätten discussed above. These beds display discontinuities of their tops, which indicates that there were variably long periods of time between pulses of sedimentation. However, relatively rapid and permanent blankets of fine-grained sediment did accumulate in some instances.

Taphofacies ID: deeper, storm-influenced shelf/ramp.—Echinoderm ossicles are common in certain bioturbated mudrocks and nodular to tabular, argillaceous carbonates and chalks (Figure 3, 6; Table 2). Some representatives of this facies display layers of nodules and bands of chert or flint that may follow contours of burrows. Silicified fossils, including echinoderm ossicles, may be present.

Most skeletal debris is highly comminuted. Echinoderm debris is among the most recognizable elements, together with some scattered shells of brachiopods, mollusks, trilobite fragments, and other fossils. Generally, only the most resistant skeletal particles belonging to Type 3 echinoderms are preserved intact. These might include calyces of microcrinoids, thecae of blastoids, and small pluricolumnals. Otherwise, the preservation is as discrete, scattered ossicles. Pelmatozoan holdfasts may occur scattered within the sediment at irregular intervals; some of these may be inverted as a result of thorough bioturbational churning of the sediment. Skeletal elements themselves are typically in reasonably good condition, with little or no abrasion, but may show some evidence for dissolution. Micritic envelopes may occur on some skeletal grains, but tend to be less common in this facies than in taphofacies IA–IC. Commonly, a certain amount of early diagenesis may have taken place leading to the development of minor impregnation of pyrite and/or glauconite.

Event beds tend to be less common in this facies, than in Taphofacies IC. However, occasional bedding planes may display articulated fossils, such as longer segments of crinoid stems, coronas of echinoids, or cups of Type 2 crinoids. The Lower Triassic Virgin Limestone sea urchin (*Miocidaris utahensis*) bed of St. George, Utah, is an excellent example of such Lagerstätten. Over 200 intact or slightly crushed imbricated tests are exquisitely preserved in the very fine-grained unit, most with both primary and secondary spines and lantern structures (Kier, 1977b). Such extraordinary preservation of the early post-Paleozoic imbricated tests indicates that were either buried alive or very soon after their demise. Likewise, some extraordinary cidaroid echinoid and crinoid assemblages occur on certain bedding planes of the Cretaceous "Chalk" in Britain. In addition, exceptionally well-preserved irregular echinoids occur in "The Chalk" at a number of levels. These latter probably represent individuals that died and were fortuitously buried within their dwelling burrows (Kier, 1977a).

Overall conditions in this taphofacies suggest long-term accumulation of skeletal debris with relatively little physical disturbance. Extensive bioturbation suggests that sediment accumulation rates were sufficiently slow to enable fossils to be thoroughly disaggregated and churned by infaunal scavengers or deposit feeders. The occurrence of associated, but partially disarticulated skeletal portions on some bedding planes indicates *in situ* decay and collapse with slow burial, but in a low-energy environment in which skeletal particles were not widely separated from one another. The relative rarity of event beds within this type of taphofacies may be the result of slow sedimentation (relative sediment starvation) and/or the position of these environments distal to storm action required to resuspend and redeposit sediments. Nonetheless, the unusual examples cited above prove that rarely fine-grained carbonate silt and mud was resuspended, probably in upslope areas, and was rapidly redeposited.

Taphofacies IE, IE': distal shelf/ramp or 'lagoonal'.—This taphofacies is comparable, in some ways, to Taphofacies ID in that it occurs in fine-grained, laminated to slightly burrowed sediments (Figures 3, 6; Table 2). However, the sediments in this case are dominantly thin-bedded, to platy, tabular and planar to vaguely cross-laminated carbonates (calcisiltites and calcilutites) that are regularly interbedded with calcareous shales or slightly argillaceous micrites. Bed bases may display minor, thin lags of coarser skeletal debris; tops may display minor burrowing.

Much of the rock is sparsely fossiliferous to barren. Echinoderm and other skeletal debris may occur on a few bedding planes as scattered, disarticulated ossicles. Well-preserved fossil assemblages, including echinoderm Lagerstätten, occur on certain undisturbed bedding planes. Most commonly, these are on undersurfaces of beds; however, examples of well-preserved crinoids may occur within beds or on upper surfaces of limestones. The skeletons in these facies tend to be well articulated, with appendages intact. Minor current alignment may be present.

Such environments seem to have been typical of two basic settings: (E') interreef and "lagoonal" settings, and (E) deep shelf to distal ramp. Unfortunately, these settings may be represented by nearly identical taphofacies and must be distinguished by other criteria, especially in the context of associated facies.

In the former case, the platy limestones represent storm beds washed off from nearby shoals (or other carbonate "factories"), which may grade laterally (or vertically in shallowing-upward successions) into peritidal facies. These environments were relatively shallow but stagnant settings subject to periodic oxygen stress at the bottom which may have been an important agent of mortality of benthic populations. Excellent examples of this sub-facies occur in the transitional facies of the Manlius and Coeymans formations of central New York (Goldring, 1923). Here, relatively low diversity assemblages of crinoids occur in gradations between echinoderm skeletal grainstone and cryptalgal laminated micrites with fenestral fabrics and desiccation cracks.

In the latter case (E), the tabular limestones are interbedded with and infinger laterally with dark gray shales. The carbonates represent carbonate sediment transported into deeper water; they may record distal carbonate storm flows or turbidites. Here, depositional environments include deeper slope or ramp settings. Density stratification of basins may result in stagnation of bottom waters and lowered oxygen levels. The result is a stressed environment that is not highly favorable to all echinoderms, but may be excellent for preservation. Excellent examples of this sub-facies occur the Middle Ordovician Rust Member of the Denley Formation (Trenton Group) near the classic Trenton Falls, New York, section. These platy limestone facies pass laterally into dark gray, calcareous ("Utica") shale. A modest diversity of articulated, primarily inadunate crinoids occurs on bases and less commonly within or on tops of calcilutites. The latter represent crinoids that were detached and redeposited in carbonate event beds. Another example is the platy limestones of the Cambrian Wheeler Formation of Utah, which yield complete specimens of the delicate eocrinoid *Gogia* (Sprinkle, 1973).

Taphofacies IF: dysoxic to anoxic carbonate basin.—This type of assemblage is associated with thin-bedded to platy, very fine-grained (lithographic) limestone to slightly argillaceous dolostone (Table 2). Disarticulated fossils are rare, but entire, articulated skeletons, parts of skeletons (e.g., crinoid arms), and even soft parts may be preserved on bedding planes. Despite generally good articulation of fossils, some echinoderm specimens in this taphofacies also may display evidence for *in situ* collapse and disarticulation. Echinoderm skeletons commonly show evidence of decalcification, in which they are preserved as poorly-defined, stained molds on bedding planes. Pyrite, typically observable in weathered slabs as limonitic stains on fossil molds, occurs as a trace mineral in some examples.

This unusual taphofacies is ideally represented (IFa) by lithographic limestones (plattenkalk facies) that were rather widespread in the Mesozoic, including the Jurassic Solnhofen Limestone of Germany. In this famous unit, the stemless crinoid, *Saccocoma*, accumulated in some numbers on certain bedding planes. Some beds may display completely laminated fabrics, indicative of anoxic bottom water conditions. Ruffled surfaces on bedding planes may represent bacterial mats that built up on quiet, undisturbed seafloors ("stagnation Lagerstätten" of Seilacher et al., 1985). Recently, *Saccocoma* has been interpreted as a benthic, mat-sticking organism that colonized the seafloor opportunistically during oxygenation events (A. Seilacher, personal communication, 1997).

The benthic environment in these settings was normally too hostile for survival, and if organisms were imported live into this environment they quickly expired (as evidenced by *Limulus* "death marches;" Seilacher et al., 1985). Preservational conditions were relatively good as a result of reduced bacterial action (even, in some cases, including anaerobic bacteria if waters were hypersaline). However, low pH conditions prevalent at the seafloor caused decalcification of carbonate skeletons. These facies appear to represent stagnant lagoonal or interreef basins.

A variant of this taphofacies would include the Silurian Mississinewa and Eramosa platy limestone beds of eastern North America (LoDuca and Brett, 1997; Tetreault, 1995). These facies are thought to represent low-energy, dysoxic to anoxic, and in some cases, slightly hyper-saline environments that were either inhospitable (like Solnhofen-type facies) or conducive only to a few species of highly tolerant echinoderms, which nonetheless populated the sea floor in some abundance within local patches. In such cases, the fossils appear to represent *in situ* populations but in some cases echinoderm remains could represent allochthonous carcasses, as in the typical Solnhofen examples.

Siliciclastic-Dominated Taphofacies

These taphofacies are characteristic of shelf settings with heavy input of terrigenous sediment. In general, environmental energy, sedimentation rate and corresponding grain size decrease offshore, whereas echinoderm abundance tends to increase. Generally higher rates of sedimentation compared to carbonate shelves/ramps favor somewhat improved preservation overall for any given depth.

Taphofacies IIA: sandy shoreface-proximal storm-dominated shelf.—Echinoderm remains may occur in scattered stringers and lenses within otherwise sparsely fossiliferous, planar, trough, and hummocky cross stratified sandstone and coarse siltstone (Figures 5, 6; Table 3). In places, echinoderm columnals, plates, and spines, as well as disarticulated and broken shells may occur as thin graded beds. Locally, these may thicken into lenticular, sandy echinoderm packstones (resembling Taphofacies IA). However, certain bedding planes within these sandstones also yield well-preserved fossils. Because of the coarse grain size and high porosity of sandstones, skeletal remains may occur as external molds in weathered outcrops. Particularly typical of these facies in the Paleozoic are certain inadunate and camerate crinoids. Rarely, complete ophiuroids or asteroids may be abundant on particular event bedding planes.

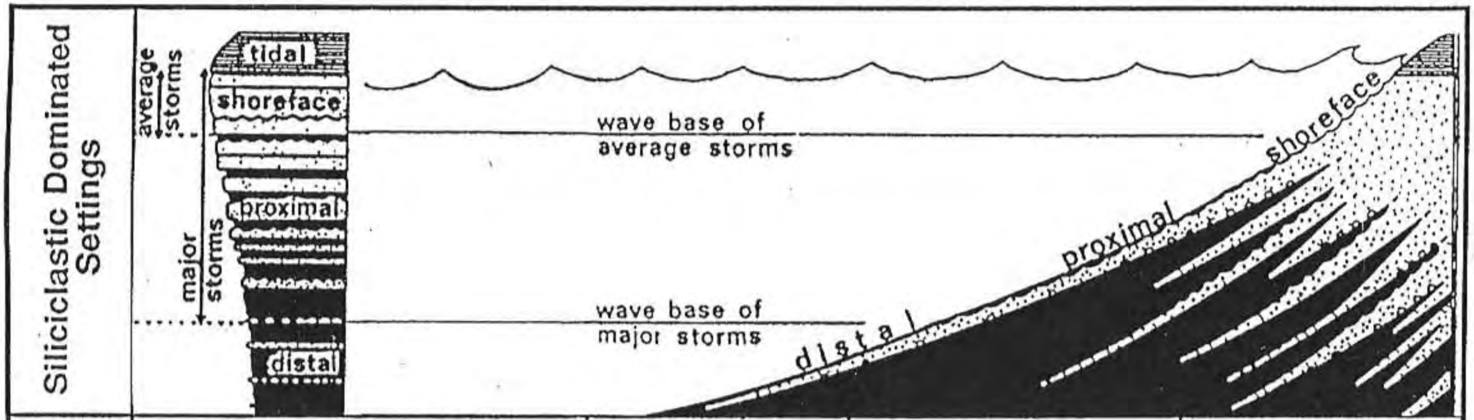
An excellent example this type of nearshore storm sand-dominated facies is the massive Oriskany (Ridgeley) Sandstone of Maryland. This unit has yielded (molds of) large crowns of camerate crinoids that were evidently detached and buried in sand during storms (Seilacher, 1968). The famed Jurassic Downcliffe Sands "starfish bed" of the Dorset coast in Britain (Goldring and Stephenson, 1972) yields well-preserved ophiuroids at the base of a hummocky cross-stratified sandstone. A similar example is provided by the Middle Devonian Mount Marion starfish bed found in a sandstone band in the Hudson Valley region of New York State, in which asteroids were buried alive, some in apparent predatory positions attached to articulated bivalves (Bishop, 1975).

The presence of trough cross-bedding in some beds suggests migration of sand waves or large ripples. These sandstones represent high-energy shoreface environments. In other cases, hummocky cross stratification indicates deposition as offshore storm-dominate shelf sands. Graded echinoderm-shelly skeletal layers represent storm-reworked coquinites of locally derived (parautochthonous) skeletal debris.

As in the case of skeletal shoals (Taphofacies IA), persistent reworking of sands probably disinterred many once-buried skeletal remains. However, layers of perfectly articulated fragile echinoderms prove that organisms occasionally were buried very abruptly by storm redeposited sands or by lateral shifting of sand waves. The high concentrations of suspended siliciclastic sediment, relatively unstable substrates, and perhaps abrasive nature of the environment may have mitigated against colonization by a majority of echinoderms. However, a few species, particularly of vagrant forms, such as asteroids and ophiuroids, and a few flexibly attached crinoids, were able to survive or even flourish in these environments.

TABLE 3—Summary of echinoderm taphofacies in siliciclastic-dominated facies . See Table 2 for references to Lagerstätten examples indicated by superscripted numbers.

TAPHOFACIES/ INFERRED ENVIRONMENT	LITHIC /TAPHONOMIC CHARACTERISTICS	LAGERSTÄTTEN TYPE AND EXAMPLES
IIA—SHOREFACE AND PROXIMAL SANDY SHELF loose, sand substrate; shallow, high energy, at or near normal wave base	thick-bedded to massive trough or hummocky cross-stratified (HCS) sandstone with articulated fossils on rare bedding planes, thin lenses of ossicles	ORISKANY TYPE Dev.: Oriskany Ss., MD[46] Mt. Marion Fm. (starfish bed), NY[5] Jur.: Down Cliff (starfish bed), England[17]
IIC—STORM-DOMINATED SILICICLASTIC SHELF/ DELTA PLATFORM soft silt to sand substrate; below normal but above storm wave base	gray, thin-bedded, siltstone, sandstone,and shales, minor graded beds with HCS, sand-filled scours and gutters may occur; lenticular skeletal debris; well-articulated and current-aligned skeletons abundant on some bedding planes	CRAWFORDSVILLE TYPE Ord.: Reedsville, PA[33] Dev.: Pilton beds, Eng.[16] Hamilton (Moscow Fm., in part), NY[15] Carb.: Sappington Fm., MT[54] Cuyahoga Fm., OH[43] Borden Group, Muldragh, Crawfordsville, IN[4, 31]
IID—STORM-INFLUENCED DEEPER SHELF/OUTER PRODELTA soft, typically calcareous, silty mud substrate, with local patches of shelly debris; low energy, near lower limit of storm wave base; low- moderate sedimentation rates (may intergrade with IIC and ID)	green to gray, commonly calcareous, bioturbated, silty mudstone or very argillaceous limestone, with thin lenses and beds of shelly debris; may contain concretions or carbonate nodules; abundant ossicles and partially articulated modules (*e.g.* intact thecae, tests); completely articulated skeletons rare	WALDRON TYPE Ord.: Benbolt Fm.[11] Bromide Fm., OK[53] Sil: Rochester Shale, NY[55] Waldron Shale, IN, TN[34] Brownsport Fm., TN[51] New Providence Shale, Button Mold Knob, KY[25] Jur.: Oxford Clay, England[46]
IIE—DISTAL SHELF/ BASIN soft mud to silt substrate; low energy; below storm wave base , but affected by gradient/turbidity currents	medium dark gray shale, siltstone, minor stringers and bedding surfaces with skeletal debris, bedding planes with perfectly preserved, articulated, *in situ* skeletons, minor pyrite coatings may be present	HUNSRUCK TYPE Camb.: Burgess Shale, B.C.[52] Sil.: Rochester Shale (*Homocrinus* bed), NY[55] Dev.: Hunsrück Slate, Ger.[47] Alfred Shale, NY[44] Miocene: Japan[0]
IIF. DYSOXIC/ ANOXIC MUDDY BASIN soft, mud substrate, low energy; restricted, low to moderate sediment rates; dysoxic to anoxic basin	dark gray, greenish and black laminated organic-rich shale; fossils rare, but complete echinoderms (mostly crinoids) and minor lenses of ossicles on certain bedding planes, commonly associated with wood	HOLZMADEN TYPE Dev.: Angola, Ohio Shale, NY, OH[38, 53] Jur.: *Posidonia* Shale Holzmaden, Germany[47] Black Ven Shale, England[49]



Tapho-facies	IIF	IIE	IID	IIC	IIA
Deposit. Setting	Stagnant Basin, Dysoxic Mud Basin	Distal Muddy Shelf/Ramp	Storm-Influenced Deeper Shelf	Storm-Dominated Distal Sandy Shelf	Storm-Dominated Shoreface, Proximal Sandy Shelf
Dominant Lithology/ Bed Geometry	dark gray, greenish and black laminated organic-rich shale	medium to dark shale and siltstone	siltstone, mudstone with thin lenses and beds of silt/shelly debris	thin-bedded sandstone, siltstone, and shales	thick-bedded to massive stratified sandstone
Prim. Sedim. Struct.	Lamination; distinct bedding planes with minor pelagic fossils	minor stringers and bedding surfaces with skeletal debris	minor thin lam. siltstones; lenses of skeletal debris and *in situ* "biostromes" of bryozoans may be present; bioturbation of mud	graded beds with HCS; silt- and sandstone beds displaying sharp bases with tool marks	trough to hummocky cross- stratified sandstone
Dominant Taph. Features	fossils rare; complete echinoderms (esp. crinoids) and minor lenses of ossicles on certain bedding planes	skeletal debris, bedding planes with perfectly preserved, art. *in situ* skeletons; pyrite coatings may be present	bioturbated abundant ossicles and partially articulated modules; complete fossils are rare	skeletal debris with some articulated and current-aligned skeletons	articulated fossils on rare bedding planes; thin lenses of ossicles

FIGURE 5—Summary diagram of echinoderm taphofacies and associated stratigraphic, sedimentologic, and taphonomic characteristics for siliciclastic environments. Environmental schematic modified from Aigner (1985)

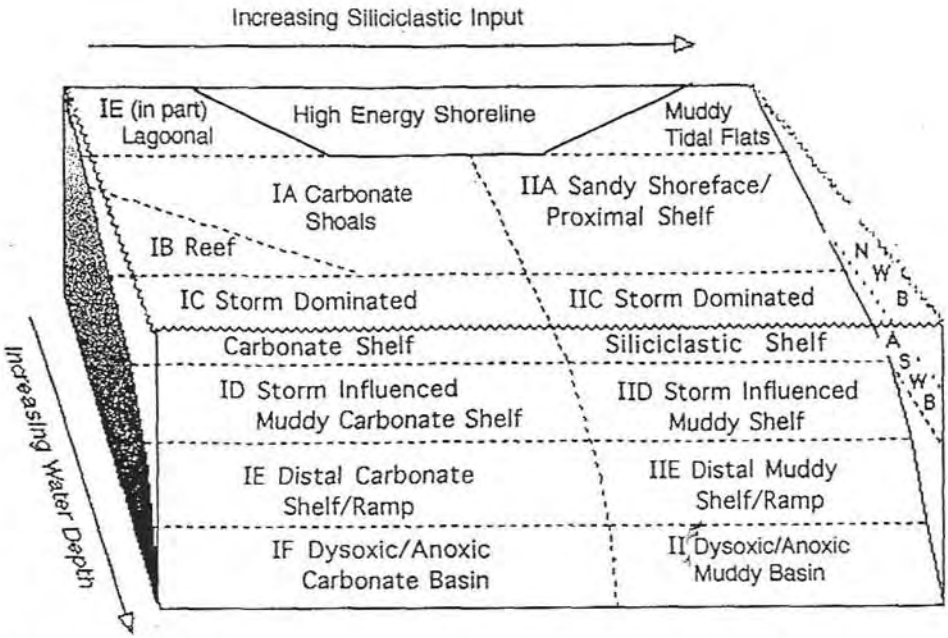


FIGURE 6—Summary diagram for environments and taphofacies of echinoderms showing relationships of adjacent facies both in relation to depth and sedimentologic factors. Taphofacies numbers and inferred environments are those discussed in text. NWB=normal wave base; ASWB=average storm wave base.

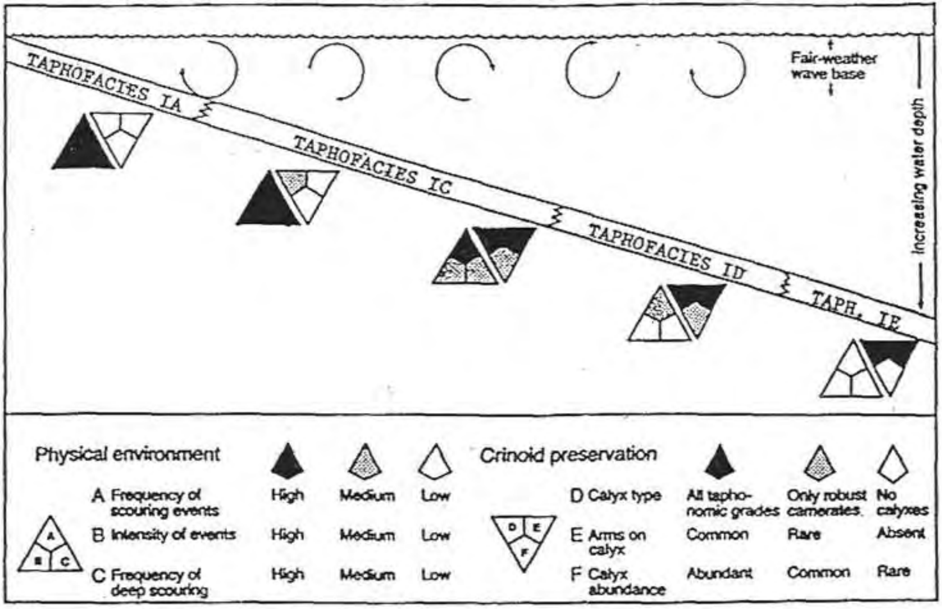


FIGURE 7—Crinoid taphofacies along an inferred environmental gradient in a mixed siliciclastic-carbonate ramp based on Lower Carboniferous Hook Head Formation, Ireland. Taphofacies designations follow the system used in this text and are equivalent to facies within the Hook Head Formation. Figure modified from Ausich and Sevastopulo (1994).

1991). Fossils are sparse and scattered in mudstone intervals, but are concentrated at particular beds or bedding planes, generally millimeters to a few centimeters in thickness.

These shelly layers may be expressed locally as very thin skeletal wacke- and packstone lithologies, but more commonly they are simply bedding plane accumulations of skeletal debris in a mudstone matrix. Within these beds, echinoderms display variable preservation. Comminuted skeletal debris is abundant, but typically unidentifiable. Plates and short pluricolumnals of pelmatozoans and/or test plates and spines of echinoids are abundant. The fossils typically are in good condition (well-calcified, little or no breakage and minor to no abrasion, corrosion, or bioerosion). Micritic envelopes are rare on echinoderm skeletal ossicles. However, epibiontic organisms, such as laminar bryozoans, may encrust some of the echinoderm debris.

In addition, certain enrichments of skeletal debris with a matrix of mudstone, may contain articulated echinoderms, depending, of course, on the type of echinoderm skeleton available for preservation (i.e., types 2 and 3). Echinoderms of Type 1 are rare or absent, except as disseminated ossicles in this taphofacies. Articulated modules of types 2 and 3 echinoderms may be common; such might include, for example, calyces of crinoids, generally lacking arms or column, thecae of cystoids and blastoids, spineless tests of echinoids, as well as long pluricolumnals (up to several centimeters in length), and *in situ* holdfasts of pelmatozoan echinoderms. The latter are most commonly represented by radices (i.e., those that display a central vertical shaft and ramifying radicles or branches). Such attachments cemented initially to hard objects, such as bryozoans, echinoderm skeletal debris, or brachiopod shells, and then ramified into soft sediment. Many of the modular skeletons of echinoderms in this facies display evidence for partial collapse. In particular, the tops of crinoid cups, or crowns, are collapsed and/or show dissociation of plates. Conversely, the under surfaces of echinoderm skeletal modules are typically much better preserved, reflecting the protective effect of coverage by sediment.

Event horizons, characterized by well-preserved, fully articulated specimens of echinoderms are relatively rare in this settings. However, occasional specimens displaying complete columns and crowns may occur, particularly at the tops of shell- or bryozoan-rich beds (Figure 2). Completely articulated specimens tend to be less common in these facies than in Taphofacies IIC. The depositional setting of these beds is similar to that observed in carbonate skeletal wackestone facies (Taphofacies IC). However, slightly higher rates of background sedimentation and/or rapid deposition of thin mud layers enabled preservation of more partially articulated skeletons. There is generally little current action on the sea floor, except during times of severe storm development. Hence, echinoderm skeletons disarticulated more or less in place, and their pieces were only dissociated slightly by gentle current action and/or the activities of benthic scavengers or infaunal bioturbating organisms, suggesting ample time for a churning and mixing of sediment by infaunal organisms. In some instances, small conical aggregations of disarticulated echinoderm ossicles may occur associated with otherwise articulated skeletons. These represent the traces of a sediment mining organism that specialized in rooting through the partially decayed skeleton bodies of echinoderms, presumably to extract organic matter for food and/or to line dwelling burrows with the skeletal remains. These traces clearly indicate *in situ* disturbance by organisms on an otherwise quiet sea floor. D

Excellent examples of IIC taphofacies occur in Paleozoic calcareous mudrocks, including the Ordovician Benbolt Formation (which contains abundant hybocrinids, see Brower and Veinus, 1978), and the Silurian Waldron (Feldman, 1989) and Rochester shales (in part; Taylor and Brett, 1996; Figure 2). Both of the latter display beds rich in skeletal debris, particularly bryozoans, brachiopods, and disarticulated echinoderms. Within these beds, more resistant modules of Type 3 and, to a lesser extent, Type 2 echinoderms may be abundant. They are generally lacking stems or arms, but individual thecae must have remained articulated and intact for considerable periods as they display encrustation over articular facets by bryozoans, worm tubes, and skeletons of other organisms. A good example of this latter type of assemblage is the Silurian Waldron Shale of the Nashville, Tennessee area, which has yielded very abundant calyces of *Eucalyptocrinites* that have been encrusted across plate sutures (and, therefore, post-mortem) by bryozoans, worm tubes, corals, and other epibionts (see Liddell and Brett, 1982). Crinoid calyces evidently remained intact long enough on the sea bottom to permit them to serve as substrates for benthic encrusting organisms (Figure 4-2). These specimens also show evidence of bio-corrosion or dissolution in what would have been exposed, uppermost portions of the upright crinoid cups. Such lines of evidence indicate that burial was not instantaneous but proceeded relatively rapidly, probably within a period of years, allowing disarticulated parts to build up and to become encrusted on the sea bottom, but not permitting complete disarticulation of such modules.

Taphofacies IIE: distal shelf/ramp.—The lithofacies associated with these occurrences typically are shale or shaley mudrock that ranges from medium to dark gray in color and contain only thin, relatively unbioturbated lags or bedding plane assemblages of skeletal debris (Figures 5, 6). Thicker beds, or biostromes, are generally absent from this facies. Bioturbation is minimal, although small burrows, such as minor *Zoophycos* and *Chondrites*, may be present to abundant (Seilacher and Hemleben, 1966). Individual bedding planes typically display debris of thoroughly disarticulated but uncorroded skeletal ossicles. For example, individual pelmatozoan columnals are common, along with some valves and even fragments of shelly organisms, such as brachiopods or mollusks. However, in many cases, these bedding planes and/or the immediately overlying nearly barren mudstone layers may display excellently preserved, fully articulated echinoderms of all types (1 to 3). They are well-calcified and display little or no breakage, minor to no abrasion, corrosion, or bioerosion, and rare micritic envelopes. Fragile forms, such as delicate, small, inadunate crinoids and ophiuroids, may be preserved intact. Certain of these forms are directly attached to objects (such as bryozoans) on the bedding planes and are thus *in situ* (Figure 2).

Very rarely, whole carcasses of echinoderms may be transported and redeposited into these environments by turbidity currents. For example, submarine fan turbidites in the Miocene near Nagoya, Japan, display complete echinoids with spines intact beneath thin decimeter-scale distal turbidites (P.A. Allison, personal communication 1997). Because the surrounding shales are sparsely fossilferous and probably represent dysoxic conditions, it is very likely that these echinoids were imported into their burial sites by turbidity currents.

Overall, these settings reflects low-energy, relatively deep-water environments that were disturbed only rarely by distal turbidity or storm-generated gradient currents. The latter permanently blanketed the sea floor with muds. Much of the muddy sediment probably consisted of silt- to fine sand-sized floccules (O'Brien et al., 1994). The presence of partially disturbed laminations, small burrows, and pyritic coatings and nodules at certain horizons suggests dysoxic, but not anoxic, conditions in the upper portion of the sediment column and at least minimal oxygenation of the sea floor.

These sorts of assemblages are among the best preserved in the fossil record. They include some of the more distal deposits of mudrock facies, such as the "*Homocrinus* beds" of the Silurian Rochester Shale, recently described by Taylor and Brett (1996). Recent work by Brett and Taylor (1997) suggests that obrution beds are preserved most frequently in sedimentary facies near the lower limit of storm wave base, where abundant benthos existed under lower energy conditions. Here, communities were smothered episodically by sediments generated from the action of storms (distal tempestites). Unfortunately, such assemblages are not representative of the optimal environmental range for most echinoderms (see Brett and Eckert, 1982), so are biased toward moderate diversity associations with rather eurytopic, generalized species.

Such assemblages also include famous conservation Lagerstätten, such as the Burgess Shale and Hunsrück Slate of Germany. In both cases, fragile echinoderms are buried essentially *in situ*, with little or no disarticulation, on top of thin skeletal debris pavements. Both the rapid and permanent accumulation of thin mud layers below even the deeper effects of storm waves and the relatively low-oxygen condition of the sediments may have aided in the lack of secondary disturbance of echinoderm skeletons in such facies.

Given the general tendency for increased bioturbation through time, especially in lower oxygen, more offshore seafloor settings (see Bottjer and Droser, 1994; Droser and Bottjer, 1993), such types of assemblages may become increasingly restricted and rare through geologic time. Many of these extraordinary echinoderm Lagerstätten deposits within mudstones are confined to the early to mid-Paleozoic era (see Aronson, 1987, 1989).

Taphofacies IIF: stagnant basin-dysoxic mud bottom.—This extraordinary echinoderm assemblage is associated with greenish-gray to black laminated shale facies, such as the Upper Devonian "Genesee facies" of eastern North America and similar Lower Jurassic (Lias) deposits of Europe (Figure 6; Table 3). Body fossils, other than those of pelagic forms, such as cephalopods, are rare and may be restricted to just a few bedding planes. Echinoderms are absent in most of the rock, but crinoids of one or two species may occur abundantly on certain bedding planes. Both disarticulated and fully articulated skeletons are preserved. Complete specimens may be coated or impregnated with pyrite. Most of these crinoids are associated with fossil carbonized logs, although skeletal debris also has been found in association with large cephalopod conchs.

Most authors have interpreted these sporadic occurrences as indicative of the sinking of pseudo-planktonic log-rafted assemblages of crinoids to an anoxic sea floor (see Wells, 1941; McIntosh, 1978; Seilacher et al., 1985; Simms, 1986). In this model, crinoids colonized rafted driftwood logs that eventually became waterlogged and sank to an anoxic sea floor. The occurrence of lenses of disarticulated ossicles overlying completely articulated crowns and columns may have resulted from incomplete burial of the crinoids. Simms (1986) noted that the lower surfaces of the Jurassic pentacrinid skeletons, like those of contemporaneous marine reptiles, are well-preserved but upper portions show evidence of disarticulation. This may indicate that the portion of the body resting directly on an anoxic substrate was protected from gentle current action or dysoxic scavengers that dissociated exposed upper parts of the carcass.

These assemblages are facies-restricted, occur only on certain extensive bedding planes, and contain many individuals. Some occurrences show evidence of more than one generation of crinoids; if all of the crinoids were pseudoplanktonic, this would require very extended floatation times for the logs. Moreover, it is difficult to explain the nearly simultaneous sinking of a large number of logs (see Brett and Seilacher, 1991 for discussion). This evidence suggests that at least some of the assemblages might represent opportunistic colonization of logs on an otherwise hostile, low-oxygen and/or sulfidic sea bottom. Many of the echinoderms in these assemblages are relatively long-stemmed crinoids that may have grown rapidly above the sea bottom such that they grew into better oxygenated, or less hydrogen sulfide-rich water that could support the adult animals. The well-preserved bedding plane assemblages still require some episodic sedimentation. Even on low-oxygen to anoxic sea bottoms, skeletons will become dissociated. Presumably, very distal turbidites or storm deposits rapidly buried these organisms' remains. Occasional bedding planes, in which only disarticulated debris occurs, associated again with logs or shells may indicate mortality of echinoderm communities that was not associated in time with pulses of rapid burial.

RELATIONSHIP OF ECHINODERM TAPHOFACIES AND LAGERSTÄTTEN TO SEDIMENTARY CYCLES

Figure 6 summarizes the relationships of the taphofacies for both siliciclastic- and carbonate-dominated depositional settings, in relation to gradients of depth- and sedimentation-related parameters. These taphofacies and their associated Lagerstätten do not occur randomly in stratigraphic sections. Rather, they form consistent and predictable series in relation to sedimentary cycles and depositional sequences. Taphofacies and the environments they represent should replace one another in predictable series both laterally (e.g., in onshore–offshore gradients) and, as a prediction of Walther's principle of facies, in vertical stratal successions. Predictable variations in depth and sedimentation patterns during typical depositional sequences and parasequences lead to regular vertical successions, which typically are not symmetrical (Brett, 1995).

Recently, two excellent studies have documented differing taphofacies of Carboniferous echinoderms (mainly crinoids) from contemporaneous facies. These semi-quantitative analyses provide excellent illustrations of the utility of the taphofacies approach. Meyer et al. (1989) developed a 9-point scale of taphonomic grades for Mississippian crinoids of the Fort Payne Formation in Kentucky and Tennessee. They then made a quantitative assessment of relative frequency of these grades in large samples from different facies in a progradational delta-front system. Meyer et al. (1989) documented distinct differences in taphofacies, ranging from mainly disarticulated ossicles in green shales near carbonate buildups to mainly complete crowns and calyces in sheet-like packstones, that could be related to environmental energy and rates of burial.

In second study, Ausich and Sevastopulo (1994) documented the varying grades of preservation of crinoids along a Lower Carboniferous (Mississippian) mixed carbonate-siliciclastic shelf and ramp from Hook Head, Ireland. They documented a gradient of differing preservational styles along the ramp (Figure 7, modified herein). Nearly complete disarticulation typified proximal crinoidal-oolitic grainstones (cf., IA, herein), best preservation occurred in mid-ramp, thin-bedded skeletal limestones with shaley partings (cf., IC, herein), and rare completely preserved crinoids in tabular-bedded calcisiltites (cf., IE, herein). Perhaps most importantly, Ausich and Sevastopulo (1994) were able to recognize cyclic variations in taphofacies within a sedimentary cycle in the Hook Head Formation. Building upon these two studies we have attempted to produce some generalized models that relate echinoderm taphofacies to depth and sedimentation parameters (Figures 7, 8). Further, we attempt to relate the occurrence of echinoderm taphofacies to predicted variations in sedimentation and water depth during deposition of sedimentary sequences and parasequences.

Taphofacies IIC: storm-dominated siliciclastic shelf/delta platform.—Echinoderm fossils may occur abundantly in heterolithic shale and thin-bedded sandstone, siltstone, and/or calcisiltite lithofacies (Figures 5, 6; Table 3). Thin-to-medium-bedded (1–30 cm in thickness), planar to hummocky cross-stratified sandstones or siltstones commonly with normal grading may be interbedded with gray mudstones or shales, in proximal examples. Beds may be lenticular in geometry and display current- or wave-rippled top surfaces. Bases are generally sharp and may show evidence of scour into underlying mudstone. Small-scale gutter casts, as well as larger sand-filled scour channels are common in these occurrences (Goldring, 1978; Goldring and Langenstrassen, 1979). Such beds typically display planar to small-scale hummocky cross stratification and burrowed tops (lam-sram fabrics; see Pemberton and MacEachern, 1997).

Fossils generally are rare and scattered in most beds. Mudrock that is interspersed with the storm calcisiltites is typically also sparsely fossiliferous to barren. However, some beds display scattered, mainly comminuted ossicles of echinoderms, convex-up valves of brachiopods, and other fossils. With increasing skeletal content, this facies may grade into Taphofacies IC.

Pelmatozoan or other echinoderm skeletal debris generally is confined to the bed soles and typically occurs as disarticulated ossicles, such as crinoid columnals. Intact skeletal modules, such as crinoid calyces or echinoid tests, are not common. However, some bedding planes yield spectacular occurrences of perfectly articulated skeletons or articulated major portions of skeletons. These assemblages may include even fragile (Type 1) remains, such as arms of crinoids and complete ophiuroids. Long sections of pelmatozoan stems may display preferred orientations parallel to groove casts. Particularly typical of Paleozoic examples are "log jams," masses of elongate crinoid columns aligned parallel to one another, commonly associated with detached crowns, arms, or other articulated portions. These represent current aggregated assemblages, probably produced by distal storm scour and redeposition (Donovan and Pickerill, 1995). Detachment of crowns and arms in some such cases may reflect physical damage during turbulence events. Internally, these event beds typically lack fossils, but may in rare instances display completely articulated echinoderms that were caught up and buried during a sedimentary event. Donovan and Pickerill (1995) described remarkable examples of apparently upright columns in Silurian mudstones of Nova Scotia. These may indicate very rapid *in situ* burial by storm muds.

An excellent, although relatively distal, example of a Lagerstatten developed within this taphofacies is the famed exposures of the Mississippian Edwardsville Formation of the Borden Group along Sugar Creek, near Crawfordsville, Indiana. Here, large aggregations of crinoids, ophiuroids, and other organisms that inhabited the outer submarine platform region of the Borden Delta were decimated and buried intact beneath silty mud layers (Lane, 1973; Ausich et al. 1979). Another well-known representation of this taphofacies is the Upper Ordovician Reedsville Formation, in which a variety of fragmentary and complete crinoids, homalozoans, ophiuroids, and asteroids occur on the bases of thin siltstones and sandstones with small-scale HCS. Concretions or nodular carbonates may be interbedded with mudstones. Burrow-mottled fabrics are characteristic of the mudstones. Mudrocks are commonly calcareous and silty.

This facies is similar to its carbonate analog, Taphofacies ID, but is characterized by a higher proportion of articulated skeletal modules (calyces, thecae, tests) and is associated with lithofacies showing higher proportion of mudstone than the latter. Typically, fossils in this taphofacies exhibit a bimodal distribution (Speyer and Brett,

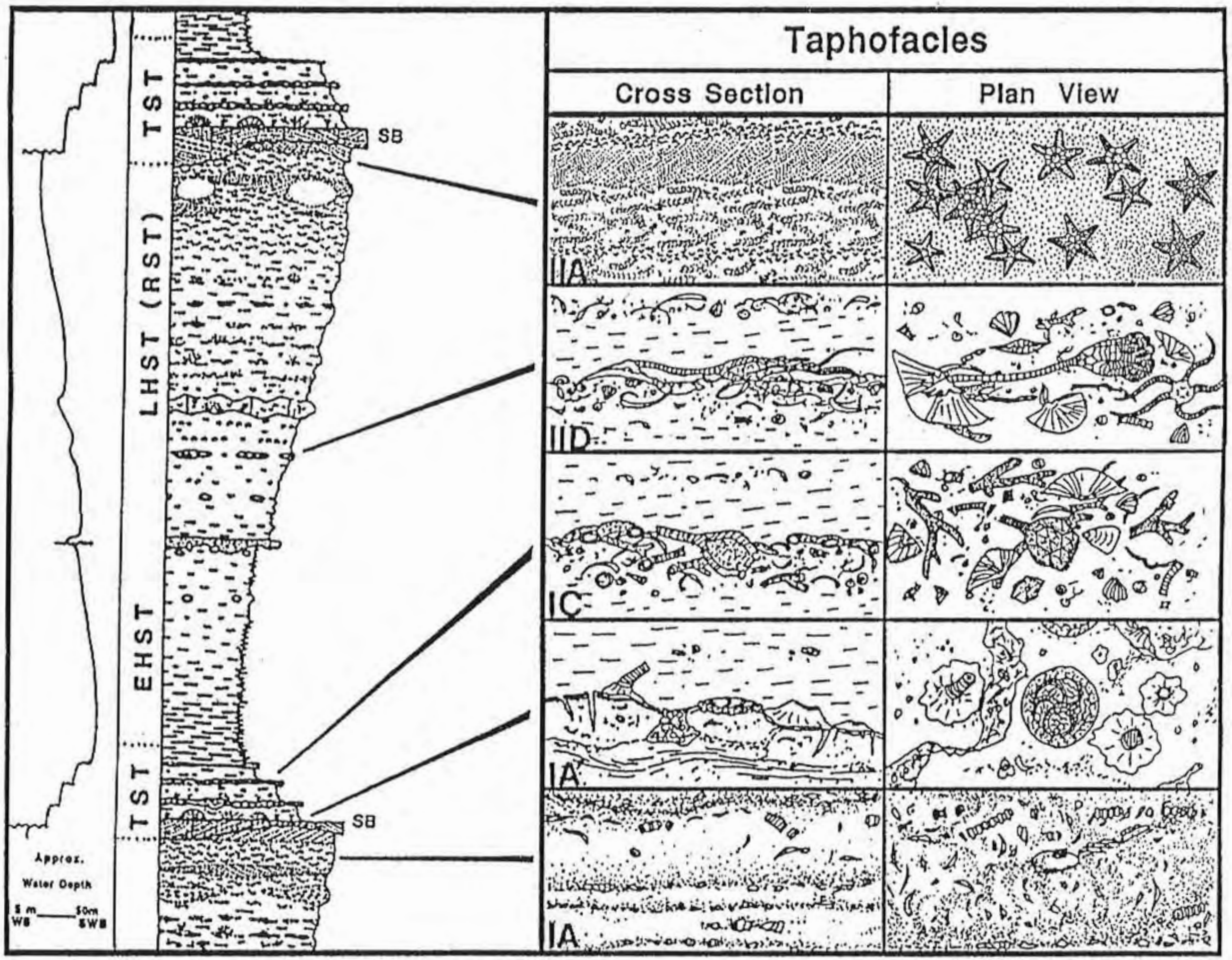


FIGURE 8—Echinoderm taphofacies and stratinomy through an idealized depositional sequence. Insets show cross-section and plan view of beds with taphofacies as indicated (see text for explanation). TST=transgressive systems tract; EHST=early high stand systems tract; LHST (RST)=late highstand systems tract (regressive systems tract); SB=sequence boundary. Depth curve on left, WB=normal wave base; SWB=storm wave base. Stratigraphic column modified from Brett and Baird (1993)

Distribution of echinoderm taphofacies in carbonate-dominated depositional sequences.—In generally carbonate-dominated successions of shallow platforms or ramps (left side of Figure 7), a typical transgressive systems tract might commence with micritic, platy limestones with Taphofacies IE' bordered by coarse skeletal shoals and, on the seaward side, minor stabilized bioherms (Taphofacies IA, IB). Considering echinoderms, specifically, the relatively shallow and non-turbid conditions associated with initial sea-level rise may favor proliferation of suspension feeders, such as crinoids and other pelmatozoans in shallow waters at or slightly below wave base. Lateral migration of high-energy shoal (shoreface) environments during transgressions may spread skeletal grainstone facies widely as slightly diachronous sheet-like deposits (Ausich, 1997). These skeletal limestones may sharply and unconformably overlie older carbonate sediments along surfaces that are combined sequence boundaries and ravinement erosion surfaces.

The condensed sections at tops of carbonate transgressive systems tracts may be ideal settings for stabilization and early cementation of older skeletal deposits to form hardgrounds of Taphofacies IA'. Because these are formed during relatively low-energy and deepening settings, they may preserve a record of the last community, commonly including attached forms such as pelmatozoans or edrioasteroids and vagrant hard substrate echinoids or starfish, as an obrution Lagerstätten (Rosenkranz, 1971). The stabilized upper surface of pelmatozoan shoal sediments also may offer an excellent surface on which biohermal development may take place. Relative increase in water depth may further promote vertical buildup of biohermal mounds or reefs, provided that the production of carbonate sediment keeps up with sea-level. Such reefal buildups and their associated echinoderm-rich flank facies (Taphofacies IB) may thus tend to occur surrounded by muddy, restricted "interreef" facies (including Taphofacies IE and IF) during early highstand phases, provided that the rate of relative sea-level rise is slow.

In other more asymmetrical cycles, transgressive echinoderm grainstone or packstone deposits are abruptly overlain by thin-bedded calcarenites (packstone-grainstone) or even platy calcisiltite and calcareous shale facies recording deeper shelf and ramp environments (Taphofacies IC or ID). These distal (late transgressive to early highstand) deposits may display biostratigraphic (e.g., mixed zones or subzones) or sedimentologic (e.g., rich in glauconite, phosphate) evidence of being relatively condensed. Nonetheless, because they may comprise little more than a stack of extraordinary event beds, condensed sections also may be an excellent area to prospect for echinoderm Lagerstätten.

The same phenomenon also may occur at the bases of smaller scale parasequences (BOP or base of parasequence beds of Kidwell, 1991, and Banerjee and Kidwell, 1991). Because these beds are associated with marine flooding surfaces they may reflect relatively sediment-starved conditions that may, again, favor colonization by pelmatozoans that require hard substrates and/or low turbidity.

Early to middle highstand carbonates in offshore areas may be represented by bioturbated, sometimes cherty micrites or chalks with generally sparse, disarticulated echinoderm debris (Taphofacies ID). Soft unstable substrates and/or some turbidity associated with bioturbation may cause a reduction in echinoderm density and attendant decrease in skeletal ossicles. These beds in turn may give way shoreward, or up section, in shallowing-upward successions to heterolithic pack- and grainstone facies (variants of Taphofacies IC) in the later highstands.

Distribution of echinoderm taphofacies in siliciclastic and mixed siliciclastic-

carbonate-dominated depositional sequences.—In siliciclastic sedimentary sequences, all echinoderm facies tend to be suppressed and less diverse and abundant. Nonetheless, in parts of the sequence, rapid input of siliciclastics may favor the highest grades of skeletal preservation. Furthermore, there may be some substitution of carbonate-(echinoderm-) dominated taphofacies in otherwise siliciclastic-dominated successions during the sediment-starved interludes of transgressions (Figure 8). A typical sequence might begin with lowstand or early transgressive sandstones, commonly massive to trough cross-bedded arenites. As noted, echinoderms tend to be rare and scattered in these settings because of substrate instability and/or siliciclastic sedimentation rates.

Taphofacies IIA accumulate only rarely because of unfavorable conditions for permanent burial in shifting sands. However, rare accumulates of ossicles or whole skeletons of a few tolerant, nearshore forms, such as a few flexibly attached crinoids, clypeasteroids, and asteroids, may be fortuitously buried and well preserved.

Later transgressive sections in many siliciclastic-dominated depositional sequences may display more fossiliferous beds, even including thin widespread sandy, skeletal limestones, or calcareous sandstones, of taphofacies IA, IIA or IIC. These facies may display variably preserved echinoderms, from highly comminuted and abraded ossicles to some complete fossils. These carbonates tend to accumulate specifically during times of terrigenous sediment starvation associated with drowning of siliciclastic shorelines and nearshore sediment sequestering. These rocks have sedimentologic and taphonomic characteristics similar to transgressive skeletal limestones in carbonate depositional systems, but they typically are thinner. As with the latter, these represent transgressive lag deposits that may overstep lowstand/ravinement erosion surfaces. They are typically the most echinoderm-rich portion of siliciclastic sequences because they form in shallow, turbulent, low-turbidity environments.

Condensed, late transgressive to earliest highstand sediments or flooding surfaces of parasequences in siliciclastic sequences may display thin-bedded heterolithic successions of fossil-rich, calcareous siltstone or even echinoderm pack- and grainstone of taphofacies IC or ID transitional to IIC or IID. These again evidently accumulated under deeper, deepening, and siliciclastic-starved conditions. As with carbonate systems, these beds typically comprise a thin, widespread interval. Only large and extraordinary depositional events may be recorded at all. Thus, despite overall condensation in this facies, the abundance of benthic organisms and lack of dilution may permit preservation of closely stacked echinoderm-rich (or other fossil-rich) Lagerstätten.

Early highstand deposits in offshore areas may show an abrupt shift to fine-grained siliciclastics. Dark-gray to black shales may dominate this portion of the sequence. Although low-oxygen/high-organic conditions near the sediment/water interface mitigate against benthic colonization, especially by echinoderms, they may also favor preservation of any organisms that happen to colonize or settle into this environment (e.g., crinoid colonies on logs). Consequently, some remarkable Holzmaden-type Lagerstätten (Taphofacies IIF) may occur in this portion of the sequence. In more shoreward sections, the early highstand may again yield abundant fossil assemblages, including some classic Lagerstätten (Taphofacies IID and IIE).

Later highstand conditions show generally coarsening- and shallowing-upward successions. Increased siliciclastic input, substrate instability and, in some areas, low oxygen, probably explain the paucity of echinoderm remains in such settings, although occasional samples of Taphofacies IID or IIE may occur at bases of parasequences (again the association with temporary lulls in sedimentation).

Finally, late highstand (regressive) to lowstand conditions display a return to heterolithic shale-siltstone or shale-sandstone successions, which may yield rare well-preserved bedding-plane assemblages of more eurytopic echinoderm taxa (Taphofacies IIC).

CONCLUDING REMARKS

Echinoderm fossils provide valuable tools for sedimentary geology and paleoenvironmental analysis. First, they are taphonomically sensitive and may provide excellent indicators of the temporal scale of particular sedimentary units (e.g., distinguishing event beds from background sediments). Second, studies such as those of Meyer et al. (1988) and Ausich and Sevastopulo (1994) indicate that comparative taphonomy of echinoderms may provide valuable clues to depositional environments and their background environmental processes. In turn, we have attempted to develop qualitative taphofacies models that may predict the occurrence of varying echinoderm taphofacies in relation to environmental gradients.

Overall, of course, echinoderms are "where you find them;" any well-preserved specimen represents a rare coincident of favorable conditions, which may occur in a wide variety of marine environments by chance. Nonetheless, the basic framework of taphofacies in relation to sequence stratigraphy should lead to better predictive models for the distribution of such echinoderms and echinoderm-derived sediments. Ultimately, this not only may aid substantially in our understanding of ancient echinoderm distribution patterns, but also possibly provide a tool for prospecting for new occurrences of these remarkable fossils.

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