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Experimental disintegration of regular echinoids: roles of temperature, oxygen, and decay thresholds

Susan M. Kidwell and Tomasz Baumiller

Abstract.—Laboratory experiments on regular echinoids indicate that low water temperatures retard organic decomposition far more effectively than anoxia, and that the primary role of anoxia in the preservation of articulated multi-element calcareous skeletons may be in excluding scavenging organisms. When tumbled at 20 rpm, specimens that were first allowed to decay for two days in warm seawater (30°C) disintegrated more than six times faster than specimens treated at room temperature (23°C) and more than an order of magnitude faster than specimens treated in cool water (11°C). In contrast, the effects of aerobic versus anerobic decay on disintegration rates were insignificant. The longer the period that specimens were allowed to decay before tumbling, the greater the rate at which specimens disintegrated, until a threshold time that appears to mark the decomposition of collagenous ligaments. This required a few days at 30°C, about two weeks at 23°C, and more than 4 weeks at 11°C for *Strongylocentrotus*. Up until this threshold, coronas disintegrate by a combination of cross-plate fractures and separation along plate sutures; cross-plate fractures thus can be taphonomic in origin and are not necessarily related to predation. Specimens decayed for longer-than-threshold periods of time disintegrate virtually instantaneously upon tumbling by sutural separation only. Undisturbed coronas can remain intact for months, sufficient time for epibiont occupation. Rates of disintegration were documented semi-quantitatively by recognizing seven stages of test disarticulation, and quantitatively by tensometer measures of test strength and toughness. The effects of temperature and oxygen on decay and the existence of a decay threshold in disintegration should apply at least in a qualitative sense to many other animals whose skeletons consist of multiple, collagen-bound elements.

Regular echinoids should still be perceived as taphonomically fragile organisms, but our results suggest the potential for latitudinal as well as bathymetric gradients in the preservation of fossil echinoid faunas. Echinoid preservation under any given set of conditions should also be a function of taxonomic differences in test construction (particularly stereom interlocking along plate sutures) as suggested by previous workers, although our experiments indicate that these effects should only be significant among post-threshold specimens. A survey of regular echinoids from Upper Cretaceous white chalk facies of Britain substantiates the basic experimental patterns, yielding examples of all disarticulation stages and significant taxonomic differences in quality of preservation. A diverse array of borers and encrusters on fossil coronas also corroborates the post-mortem persistence of some tests on mid-latitude seafloors.

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Introduction

It has been argued that the poor record of regular urchins reflects low preservation potential rather than low original abundance (Kier 1977), but little actualistic information is available on rates and controls of skeletal disintegration for these fragile epifauna. Most data for echinoids—as for most non-molluscan invertebrates—are anecdotal. The major exception has been Schäfer's qualitative experiments of more than 30 years ago (summarized in Schäfer 1972). He found that tests of the regular echinoid *Echinus* disintegrated within two weeks in quiet (presumably aer-

ated) water and in less time if disturbed by benthic scavengers, and outlined the sequence of post-mortem disarticulation. After pedicellariae and spines detach, the peristomial and periproctal membranes disintegrate, the lantern disarticulates, the apical system collapses and finally the corona splits along plate sutures as connective tissues (collagenous fibers) decay.

These and similar actualistic observations (D. Nichols pers. comm. in Aslin 1968; Ernst et al. 1973; Kier 1977: pp. 170–171; Smith 1984) and circumstantial evidence from the fossil record (complete specimens rare, and these

commonly associated with sedimentologic evidence for catastrophic burial or seafloor anoxia; Zullo et al. 1964; Bantz 1969; Bloos 1973) suggest that good preservation of regular echinoids, like that of many other echinoderms (Linck 1965; Meyer 1971; Liddell 1975; Lewis 1980; Meyer and Meyer 1986; Jensen and Thomsen 1987), is unlikely barring unusual circumstances. Rapid disintegration is contradicted however by post-mortem encrustations of intact, empty coronas of thin-shelled echinoids in Recent environments (e.g., *Meoma* and *Tripneustes* in backreef and forereef environments of Discovery Bay, Jamaica [pers. obs.]; *Spatangus* and *Echinocardium* on shallow-water Mediterranean seafloor [Ernst et al. 1973]). These articulated coronas must have survived exposure on the seafloor for one or more seasons to serve as substrata for epibionts.

The details of test construction and post-mortem conditions other than burial thus clearly can retard or even halt decomposition of regular echinoid carcasses before complete disintegration. These observations and a supply of carcasses from DNA-DNA hybridization work by others at the University of Chicago and from various student projects at Friday Harbor Marine Laboratory inspired us to resume Schäfer's experiments under more controlled conditions. Specifically, we determined rates and patterns of test disintegration as a function of water temperature and oxygenation during decay, simulated transport (tumbling) and period of decay before transport. We initially used specimens of the western Atlantic regular urchin *Arbacia punctulata* to develop basic experimental procedures. For quantitative studies we shifted to two species of the regular echinoid *Strongylocentrotus* (Boreal *S. droebachiensis* and east Pacific *S. purpuratus*) that could be acquired in large numbers. Comparable experiments on other regular and irregular orders await an adequate stockpile of carcasses.

Preliminary Studies of *Arbacia*

Frozen specimens of *A. punctulata* (2.7 to 4.2 cm diameter), thawed to room temperature, were allowed to disintegrate in unagitated seawater under nine different temper-

ature-oxygen arrangements (Kidwell and Baumiller 1989). Stages of disintegration were the same as reported by Schäfer (1972), but rates varied strongly with temperature. Specimens in warm water disintegrated more rapidly (total spine loss in less than one week) than those in room temperature and cold water (spine loss in 3 weeks to more than 10 weeks, respectively). Aeration did not have a detectable effect.

These results indicated that decay in warm water was the only practical way to test the differential preservation potential of species on laboratory time scales. The persistence of intact coronas for more than 10 weeks even in warm aerated water indicated that agitation would also be essential to completing experiments within reasonable periods of time.

Effect of Decay on Disintegration of *Strongylocentrotus*

Experimental Method.—Of the two *Strongylocentrotus* species investigated, *S. purpuratus* has a more robust corona and thicker, stubbier spines than *S. droebachiensis*. They are otherwise similar in size and body shape. Thawed carcasses did not behave significantly differently from newly dead carcasses in control experiments, and thus most of our experiments were conducted using specimens that had been frozen. Freezing allowed us to stockpile sufficient numbers of similarly sized individuals for experimental runs and provided a quick, humane means of sacrificing moribund individuals. Experimental specimens ranged in size from 4.9 to 7.0 cm in diameter.

Carcasses were allowed to decay completely immersed in artificial seawater (Instant Ocean) for periods of up to five weeks at controlled temperature and oxygen levels. The tanks were kept dark at all times except for photography (we inadvertently discovered during *Arbacia* experiments that light promotes the formation of algal "jackets," which inhibit decomposition and disintegration; Kidwell and Baumiller 1989) and were inoculated with seawater from several tanks with live individuals to insure the presence of bacteria. After a set period of decay, spec-

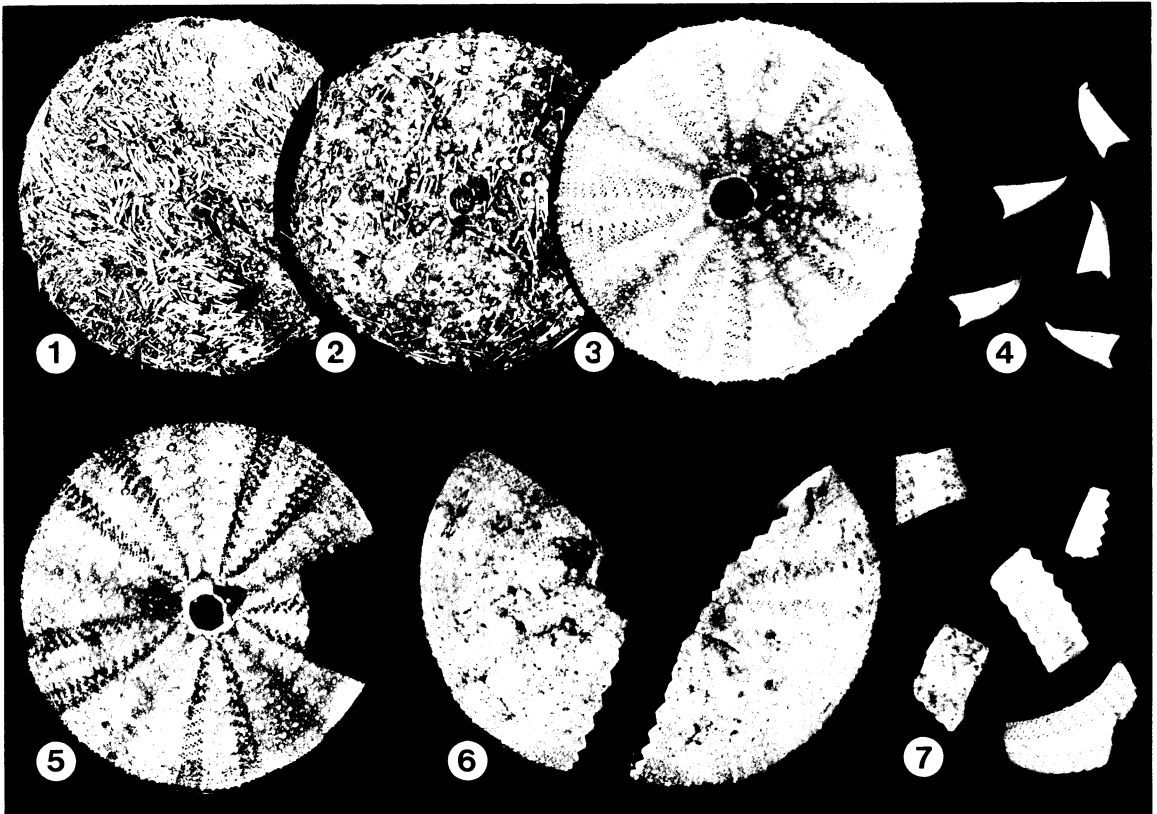


FIGURE 1. States in the experimental disintegration of the regular echinoid *Strongylocentrotus purpuratus*.

imens were tumbled in room temperature tap water at 20 rpm for up to 150 hours. Fresh water was used to slow or halt further decomposition during tumbling and was replaced every few hours. The tumbler consisted of two 15-cm-diameter gallon glass jars arranged side-by-side so that two experiments could be run simultaneously; these rested on rollers (surplus typewriter platens) driven by an electric motor. Each jar was fitted with a 2.5-cm-wide baffle or shelf, so that the carcasses would tumble once per rotation rather than simply slide around the outer wall.

Rates of echinoid disintegration were evaluated semi-quantitatively using a scale developed from preliminary experiments on *Arbacia* (Figs. 1 and 2). Seven stages were discriminated (excluding stage 0 = complete freshly dead or thawed carcass). When left undisturbed, specimens first lose spines (stage 1 or 2 depending upon extent of loss) and then the oral and aboral membranes (stage

3). Next the lantern disarticulates and falls out of the test (stage 4), leaving a hollow, spineless corona. If the specimen is tumbled, further stages of disintegration are reached: the test fractures or is punctured but otherwise remains intact (stage 5), breaks into two or more large pieces (stage 6) and finally breaks into numerous small fragments (stage 7). Specimens do not necessarily go through all stages of disintegration. For example, fresh specimens and specimens undergoing cold-water decay commonly jump directly to stage 5 or 6 during tumbling before losing all spines or their lantern.

Behavior of Fresh Carcasses During Tumbling.—The progressive disintegration of fresh specimens (zero period of decay before tumbling) of *S. droebachiensis* and *S. purpuratus* is quite distinct from that of decayed specimens. Within the first hour of tumbling, fresh *S. droebachiensis* lost all spines in some patches; after 7 hours it had lost more than half its

SEMI-QUANTITATIVE SCALE OF ECHINOID DISINTEGRATION







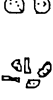
- 1. More than 50% spines on test 
- 2. Less than 50% spines on test 
- 3. Oral & aboral membranes lost 
- 4. Lantern disarticulated and out of test; empty corona 
- 5. Corona fractured or damaged 
- 6. Corona broken into large pieces 
- 7. Corona broken into small fragments or dissociated plates 

FIGURE 2. Definitions of disintegration states. Specimens do not necessarily go through all states, nor do they always go through states in numerical order.

spines and suffered some small side punctures (stage 5), compared with *S. purpuratus* which still retained most spines. By 18 hours, *S. droebachiensis* was completely denuded and had split equatorially (stage 6) and *S. purpuratus*, although retaining many spines, had suffered a major side puncture (stage 5). The specimens remained in these states with only minor change during the next 70 hours of tumbling: one hemisphere of *S. droebachiensis*

was gradually reduced in size, and *S. purpuratus* suffered additional punctures and spine loss (Fig. 3). The lanterns did not fall out until 100 hours of tumbling. During the next 30 hours of tumbling, both specimens moved into stage 6 or 7 of disintegration.

Among fresh carcasses, equatorial splits and punctures were the most common styles of breakage and almost all fractures and breaks were across plates rather than along plate sutures. It is clear that fresh carcasses of these species are extremely tough, capable of surviving considerable agitation and/or transport before breaking into small fragments.

Behavior of Partially Decayed Specimens During Tumbling.—Disintegration is measurably accelerated when specimens are allowed to decay before tumbling. For example, after 15 days of decay at room temperature (23°C), *S. droebachiensis* is a spineless empty corona (state 4) and *S. purpuratus* has lost oral and aboral membranes (stage 3) even before tumbling. After only 30 minutes of tumbling, *S. droebachiensis* suffered a major side puncture (stage 5) representing a 14-fold acceleration over fresh carcasses, which required 7 hours of tumbling to reach the same state, and by 3 hours was reduced to a single large coronal fragment (state 6). *S. purpuratus* lost most spines and reached stage 5 after one hour of tumbling, an 18-fold acceleration over fresh

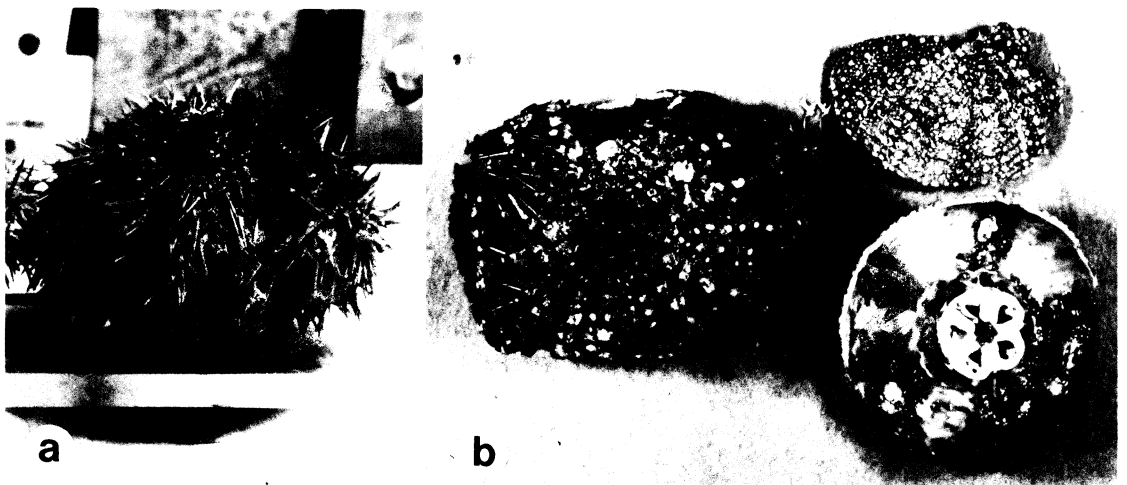


FIGURE 3. Effects of tumbling (in fresh water, no grit) on fresh carcasses. a, *S. droebachiensis* before tumbling. b, by 18 hours, *S. droebachiensis* (right) split equatorially (state 6) but retained its lantern and *S. purpuratus* (left) suffered side punctures (state 5) but retained its lantern and some spines; photograph of specimens after 44 hours of tumbling. Disintegration is largely by fractures across coronal plates.

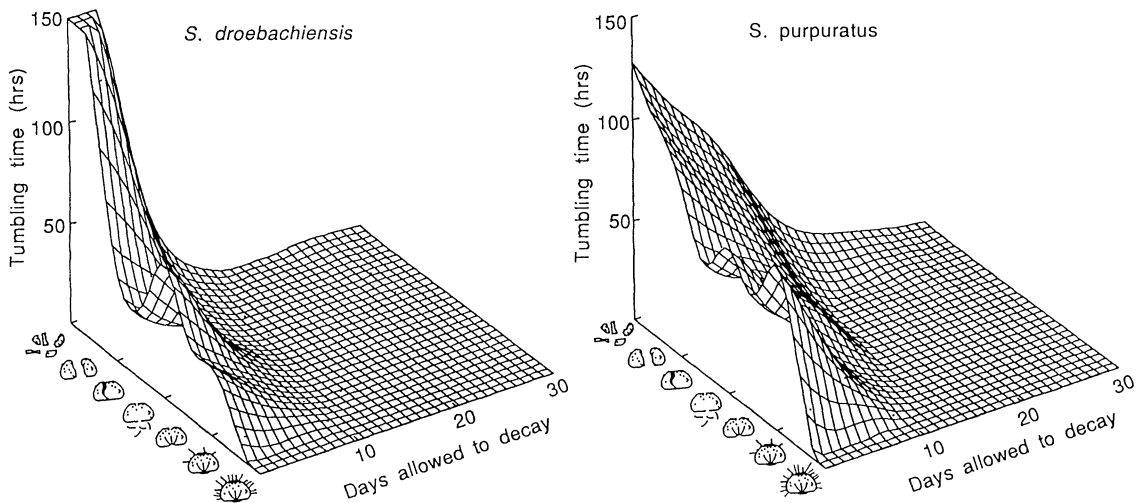


FIGURE 4. In aerated 23°C seawater, the period of undisturbed decay radically accelerates the disintegration of carcasses during tumbling up to a threshold period of about two weeks. Carcasses allowed to decay for more than two weeks all disintegrate virtually instantaneously upon tumbling, as indicated by the flattened curves. Reversals in slope in the graphs (particularly pronounced for fresh carcasses, i.e., decay time = 0) are partly due to carcasses skipping some states of disintegration (e.g., not losing the lantern until after the corona breaks apart) and are partly artefacts of the kriging algorithm (see text). Stages of disintegration as in Figs. 1 and 2.

carcasses, and reached state 6 in 15 hours or less. In contrast to fresh carcasses, partially decayed specimens broke up both by cross-plate fractures and by separation along plate sutures.

This acceleration in test disintegration probably reflects (a) reduction in the strength of ligaments between plates owing to microbial decay and (b) possibly the loss of spines, which might otherwise act as shock absorbers during tumbling (e.g., as suggested for live echinoids; Strathmann 1981). Ligamental strength is clearly still considerable, however, even after two weeks of decay, because coronas broke across plates as readily as along plate boundaries. The remanent strength of collagenous ligaments is also indicated by the abraded edges of large coronal fragments.

Threshold Effect in Rate of Test Disintegration.—As the period of decay is increased, tests disintegrate at ever faster rates during tumbling. Tumbling time required for *S. droebachiensis* to reach various stages of disintegration is plotted against time of pre-tumbling decay (room temperature, 23°C) in Fig. 4. The curve is very steep for fresh specimens (zero decay) but is much lower for specimens first allowed to decay for only a few days. The irregular

topography of the surface in Figs. 4a and 4b is due to echinoids skipping some stages in disintegration. For example, the lantern may not disarticulate and fall out (state 4) until after the corona fractures (state 5) or breaks (state 6). Some slope reversals are also partly an artifact on the kriging program (SYSTAT: algorithm by McLain 1974) in which every patch on the surface requires four weighted multiple regressions on the points, but does not require that the surface intersects all data points.

The most important feature of this graph is the flattening of the curve after a decay period of about two weeks. Specimens allowed to disintegrate undisturbed for two weeks or more at 23°C fall apart more than one to two orders of magnitude faster than fresh carcasses, that is virtually immediately upon tumbling. The same relationship was observed for specimens of *S. purpuratus* (Fig. 4). The lower slope and the convex shape of the disintegration curve between zero and two weeks of decay, as contrasted with the concave curve for *S. droebachiensis*, indicates that *S. purpuratus* is more resistant to disintegration in the initial (pre-threshold) post-mortem period.

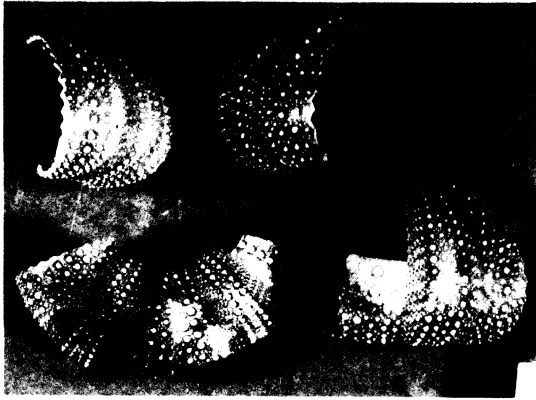


FIGURE 5. After four weeks of decay in aerated 23°C seawater, *S. purpuratus* (right) was reduced to large fragments (state 6) within 40 minutes and *S. droebachiensis* (left) within 65 minutes. Coronas disintegrated by separating along plate sutures, owing to decay of collagenous ligaments; photographed after 1.8 hours of tumbling.

We believe that the two-week threshold in the rate of test disintegration at 23°C reflects the decay time of connective tissues (collagenous ligamentary fibers) between plates in the corona. *Strongylocentrotus* specimens allowed to decay for more than two weeks not only disintegrate many times faster than fresher carcasses (Fig. 4, Table 1), but their plates separate along sutures or plate boundaries rather than breaking across plates. Differences in the behavior of pre-threshold specimens (cross-plate fracture, or a combination of cross-plate fracture and sutural separation) and post-threshold specimens (separation along plate sutures only) are apparent by comparing photographs in Fig. 3 with those of Fig. 5.

Temperature versus Oxygen Controls on Rate of Decay

Experimental Method.—In order to rank the effect of decay conditions on test preservation, thawed specimens of *S. purpuratus* were allowed to decay in darkened, inoculated artificial seawater for two days under set conditions of water temperature and oxygenation and then tumbled. Temperatures were maintained either at 11°C (cold bath), 23°C (room temperature) or 30°C (warm bath) during decay. All tumbling proceeded in room temperature tap water, which was replaced

TABLE 1. When echinoid carcasses are allowed to decay prior to tumbling, there is a threshold decay time (about 2 weeks at 23°C) beyond which tests break up almost immediately upon tumbling and fail by separating along sutures.* Data for 10 days of decay.

Decay time at 23°C	Tumbling time to reach state 6 (in hours)		Break pattern	
	<i>S. droebachiensis</i>	<i>S. purpuratus</i>	Fracture across plates	Separate along suture
Fresh (0)	18:30	120:00	XX	X
1 week	<5:00*	8:00	X	X
2 weeks	:15	<1:15	X	X-XX
3 weeks	—	:15		XX
4 weeks	<:40	<:40		XX
5 weeks	<:08	<:10		XX

every one to two hours to minimize further decay during tumbling.

We initially investigated three setups for oxygenation, as in the *Arbacia* experiments: (1) active aeration using a micropore bubbler, (2) container open to atmosphere but without a bubbler and (3) silicone sealed container. We found however that oxygen levels in the open containers were indistinguishable from those in the sealed containers based on Winkler titrations (Fig. 6) and so we simplified the experiment to a six-way test of three temperatures and two oxygen levels (actively aerated versus sealed tanks). The dissolved oxygen levels we investigated are within the range of natural seawater (0–9 ml/l; Richards 1957).

The oxygen demand of a single 6.5-gram *Strongylocentrotus* carcass in a 4-liter container was so great that freshly made artificial seawater (initial oxygen content same as tap water) was reduced to an anoxic state in less than 24 hours. We therefore did not deoxygenate seawater before starting the experiments on rates of anaerobic decay. Oxygen concentrations of fluids within carcasses were not tested and quite possibly were anoxic in all setups. For the aerated setups, however, we can be confident that at least those tissues covering the outer surface of the test were subject to aerobic decay.

Results.—After two days of decay without any agitation, specimens had already disintegrated to different states (Fig. 7, a). Specimens kept in cold water were still quite fresh in appearance (stage 1), room temperature specimens had lost a few spines and suffered

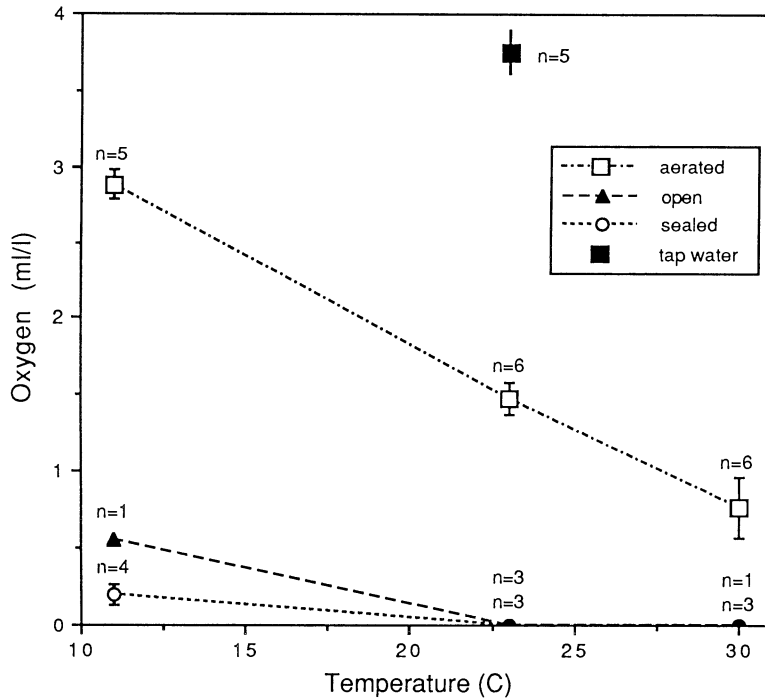


FIGURE 6. Oxygen levels in experimental tanks as a function of temperature, measured after 3 weeks of echinoid decay. Note that oxygen levels in open and sealed tanks are indistinguishable except at 11°C. n = number of samples. \pm error bars = 1 standard error of the mean.

some damage to aboral and oral membranes (stage 1), but warm temperature specimens had already lost many spines, both membranes and the lantern (stage 4). Differences became even more pronounced after the specimens had been tumbled for a few hours (Fig. 7, b-d). After 13 hours of tumbling, room temperature specimens reached stage 6 six times slower than warm temperature specimens reached the same stage. Throughout the experiment, cold water specimens behaved as fresh carcasses despite the initial two days of decay.

These results are summarized in Fig. 8a, where tumbling time is plotted against water temperature for two days of decay. Carcasses allowed to decay in warm water clearly disintegrated several times faster upon tumbling than specimens held in room temperature and cold waters. The accelerating effect of higher temperature is even more marked when the decay period is lengthened: after three weeks of decay, carcasses held in cold water still behave as if fresh, whereas room temperature carcasses fall apart about as quickly as warm

temperature carcasses upon tumbling (Fig. 8, b). These results show (a) that regardless of temperature of decay, all post-threshold carcasses disintegrate rapidly whatever the threshold period may be, and (b) that the threshold period for cold-water (11°C or less) decay of collagenous ligaments is at the very least a month or more (4-week persistence of *Strongylocentrotus coronas*, and 10-week persistence of *Arbacia coronas*) and possibly years in colder waters—that is, ecologically significant periods of time.

Figure 7 suggests that specimens held in aerated waters (lower row) disintegrated at slightly faster rates than specimens held at the same temperature in anoxic waters (upper row), but these effects turned out to be statistically insignificant after replicate runs (Fig. 9). Aerobic decomposition did not significantly accelerate test disintegration at any given water temperature; put another way, anoxic waters do not significantly retard decomposition and disintegration. Temperature was by far the more important control of disintegration rates for *S. purpuratus* under lab-

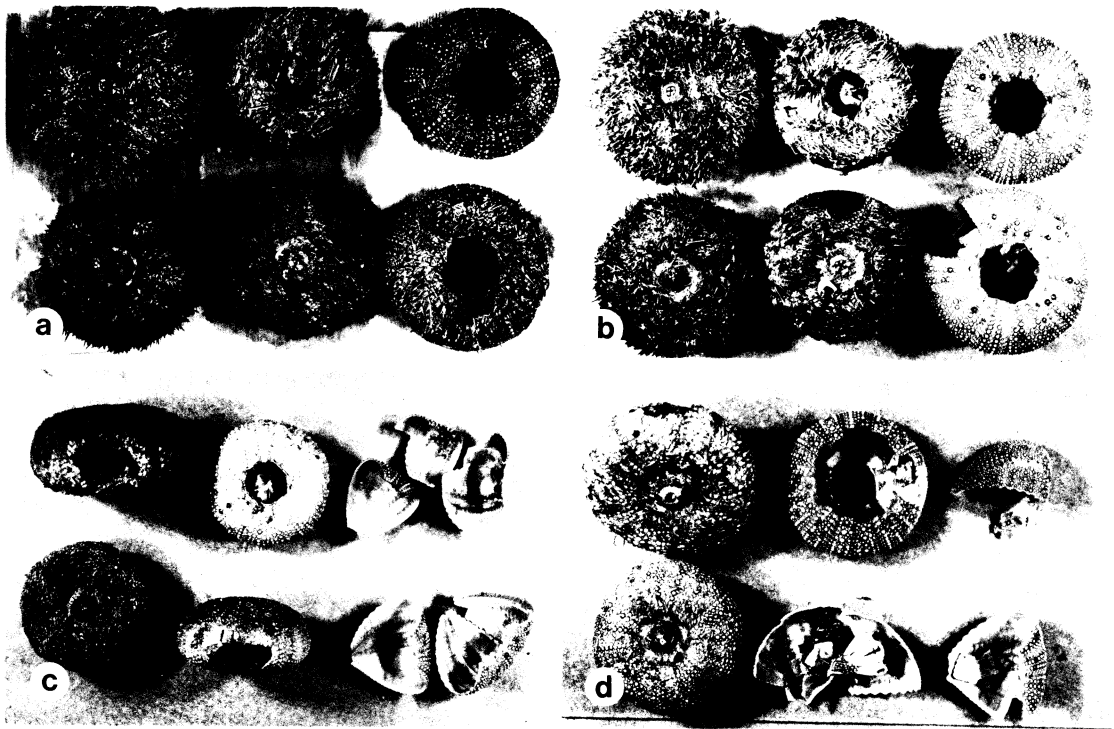


FIGURE 7. Relative effects of oxygenation and temperature of seawater on the disintegration of *S. purpuratus*; carcasses allowed to decay for two days in sealed (upper row) and aerated (lower row) tanks held at 11°, 23° or 30°C (left to right in each photograph). a, carcasses before tumbling; warm water specimens are already state 4 empty coronas. b, after 1 hour of tumbling. c, after 3.8 hours of tumbling. d, after 7.7 hours of tumbling, warm water specimens have been reduced to single large fragments (state 6) by cross-plate fracture and sutural separation, whereas cold water specimens still retain lanterns, parts of membranes and some spines (state 2) ± cross-plate punctures or fractures (state 5). Data plotted in Fig. 8.

oratory conditions (i.e., absence of predators and scavengers).

Quantitative Effects of Decay on Test Strength

In order to quantify the effects of temperature, decay time, and oxygen concentration on test strength and thereby evaluate our semi-quantitative observations, we ran a series of crushing tests on carcasses using a Monsanto tensometer. Specimens of *S. purpuratus* were placed with the oral-aboral axis parallel to the crushing plates of the tensometer (perpendicular to applied stress). A force, slowly applied to the test by displacement of the crushing plates, was continuously recorded along the x -axis of a chart recorder; displacement was simultaneously recorded along the y -axis (Fig. 10). Force was applied until the test disintegrated into several fragments.

Specimens from different treatments exhibited different patterns of failure just as in the tumbling experiments. Fresh tests and those held at cold temperatures for periods up to 4 weeks failed by either cracking equatorially and splitting into two halves or by having a hole punctured into the test at the point of contact with the crusher. Fracture occurred most commonly across the plates of echinoid tests. Specimens held at warm temperatures (23 or 30°C) for more than two weeks (i.e., post-threshold specimens) disintegrated completely into many small fragments by failing along plate sutures.

Because of the differences in the pattern of failure, a common point of reference on the force-displacement chart had to be chosen for purposes of comparison. Operationally, "test strength" was defined as the maximum force recorded and "test toughness" as the area un-

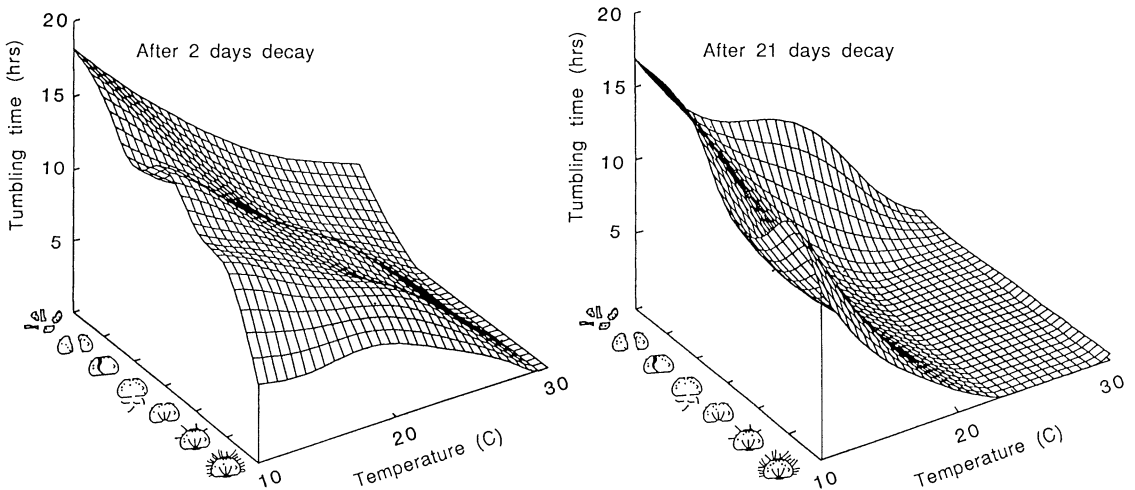


FIGURE 8. Carcasses of *S. purpuratus* allowed to decay in 23° and 30°C seawater disintegrate more rapidly upon tumbling than carcasses held in cold water (11°C), and this effect is magnified as the period of undisturbed decay is increased. After only two days of decay, carcasses held at 30°C exhibit post-threshold behavior (disintegration of corona within minutes of tumbling, failure by sutural separation). Specimens held at 23°C show this post-threshold behavior after about two weeks of decay, but cold water specimens still behave like fresh carcasses even after three weeks of decay (corona breaks before loss of lantern and/or membranes, failure by cross-plate fractures).

der the force-displacement curve between the origin and the point of maximum force (Fig. 10). This second parameter represents the sum of energy (work) applied up to the point of fracture (test strength), and is expressed in units of energy (ergs).

Due to the relatively small sample sizes and design of the experiment, a three-way ANOVA could not be used to determine the simultaneous effects of all three factors on test strength and toughness. Instead, the effect of decay time had to be examined separately, with temperature and oxygen held constant. Results of simple linear regression reveal that decay time has a significant effect on both strength and toughness ($P < 0.05$ and $P < 0.01$ respectively, two-tailed t -test). This effect can be seen in Fig. 11 (left) in which the two-week decay threshold at 23°C, mentioned in the previous section, can also be seen.

The stippled regions in Fig. 11 correspond to the average strengths (\pm one standard error) of individual plates of *S. purpuratus*. These were tested in compression both parallel and perpendicular to their long axes. Fresh carcass strength (135 Newtons \pm 36 N, 1 s or 1 SD) is comparable to the strength of single plates, whereas carcasses decayed for more than two weeks are weaker (18 N \pm 3.9 N, 1

s or 1 SD) than the weakest plates. These results are entirely consistent with the observed fracture patterns: fresh specimens break up largely by cross-plate fracture whereas post-threshold decayed specimens disarticulate along plate sutures so that individual plates remain unbroken.

Differences in test strength and test toughness were tested for the effects of temperature

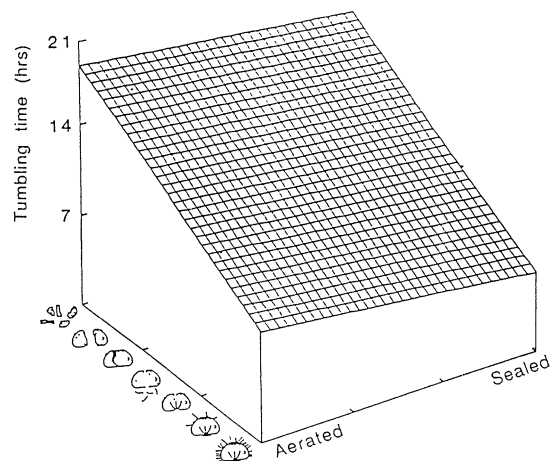


FIGURE 9. Although oxygenation appears to have some effect on disintegration rate in the photographs of Fig. 7, the effects are not significant. Kriged data are for specimens tumbled after 2 days of decay at 11°C.

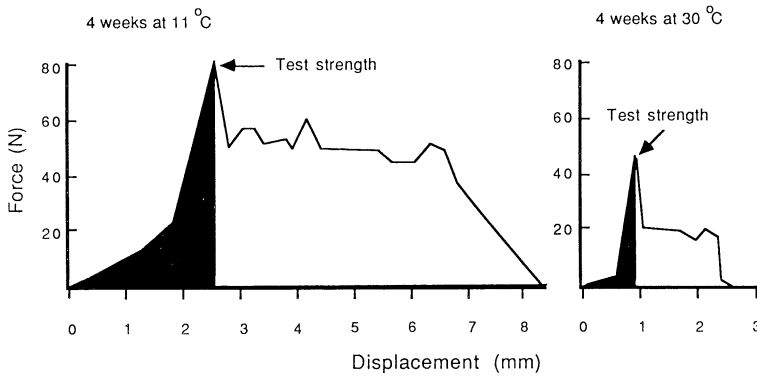


FIGURE 10. Two examples of data collected with tensometer. "Test strength," as defined in text, corresponds to maximum force applied (measured in Newtons); "test toughness" corresponds to area under the force \times displacement curve between origin and test strength (black area; measured in ergs). Results are for individual *S. purpuratus* allowed to decay undisturbed for four weeks at 11°C and 30°C (open tanks).

and oxygen concentration using a two-way ANOVA (Sokal and Rohlf 1981) with decay time held constant (Table 2). Both strength and toughness show a significant temperature effect ($P < 0.05$ and $P < 0.01$ respectively); no significant differences exist between the oxygen treatments ($P > 0.1$ in both cases). The effect of temperature is demonstrated graphically in Fig. 11 (right).

Summary and Implications of Experimental Results

The progressive disintegration of whole echinoid tests by organic decay is fairly systematic as reported by Schäfer (1972): spines are generally lost first, then membranes and lantern, followed by breakup of the corona. The sequence of mechanical damage for fresh carcasses, whether newly dead or maintained in fresh condition by low water temperatures, is quite different: the corona is commonly punctured or split before loss of spines, and the lantern can remain attached to fairly small coronal fragments.

Inasmuch as many (and perhaps most) echinoids die from conditions that inflict little mechanical damage themselves (e.g., senescence, high temperature, desiccation, and microbial "pestilence" such as the 1983 pan-Caribbean die-off of *Diadema*; Ernst et al. 1973; Smith 1984; Lessios et al. 1984; Liddell and Ohlhorst 1986; Greenstein 1989b), many carcasses in natural systems will be virtually intact at the start of the post-mortem period (i.e.,

in state 1 or 2). Even some predators, which generally account for only a small proportion of deaths in individual populations (Smith 1984), can leave relatively intact coronas (e.g., starfish which leave denuded coronas [state 4]; fish, birds and crabs that attack through the peristome [state 4 with spines intact]; drilling gastropods and, possibly, octopods [state 1 or 2 with small drillhole]; Smith 1984; Bromley pers. comm.). All of these carcasses could be expected to disintegrate as in our laboratory, as a function of period and temperature of decay.

Importance of Decay Time.—Post-mortem damage of regular echinoid carcasses during tumbling increases with the duration of pre-tumbling decay. Specimens allowed to decay for two days in warm water before tumbling disintegrated about one order of magnitude faster than fresh carcasses; longer periods of decay accelerated disintegration rates still further.

These experiments extend Allison's (1986) work on polychaetes and arthropods to animals with fully mineralized skeletons, and support his finding that quality of preservation can be a poor index of post-mortem transport. If carcasses disturbed soon after death are less likely to break or disarticulate than carcasses allowed to decay for some period, then the stage of disarticulation of multi-element skeletons is an unreliable guide to distance of transport or energy of reworking events.

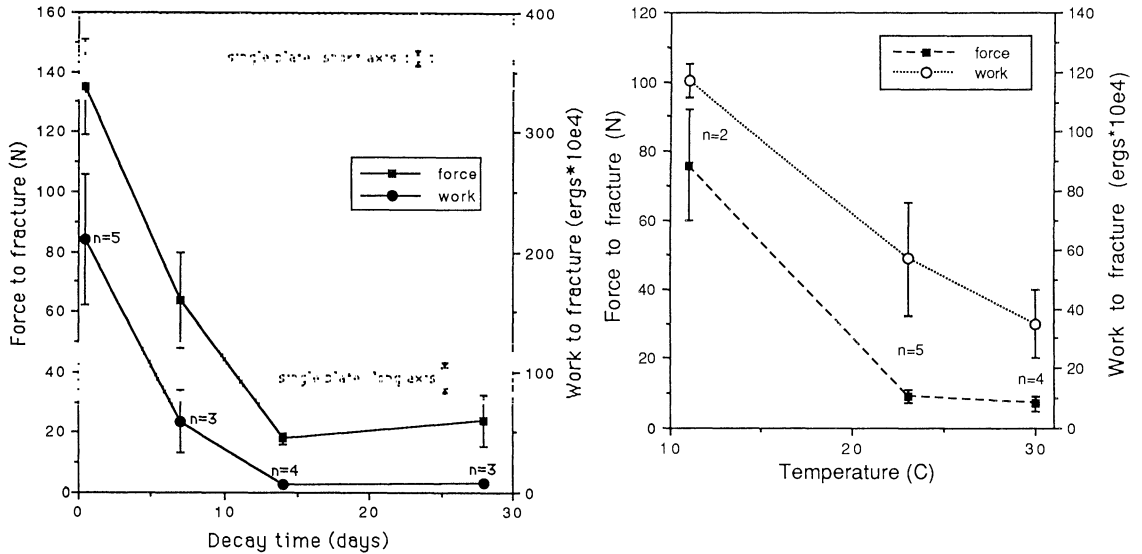


FIGURE 11. Left, quantitative effect of decay time on test strength and test toughness for *S. purpuratus* allowed to decay undisturbed at 23°C in open tanks. Stippled bands indicate force required to fracture single plates. Right, quantitative effect of temperature on test strength and test toughness for *S. purpuratus* allowed to decay undisturbed in open tanks for 4 weeks. N = number of samples. Measurements of force to fracture and of work to fracture were obtained from the same specimens. Error bars = ± 1 standard error of the mean.

Disarticulation instead reflects the time lag between death and physical disturbance of the carcass, whether disturbance be in the form of out-of-habitat transport, within-habitat rolling about, erosional exhumation or manipulation by organisms. The exact period of time over which a carcass can survive physical disturbance without disintegrating—the time window of “invulnerability”—depends upon the temperature of decay (see point 3 below) and on details of skeletal construction that inhibit disintegration even after collagen decay (e.g., interlocking stereom at sutures). These three factors then—time for decay, temperature of decay, and type of hardpart articulation—determine the accuracy with

which the preservational state of multi-element skeletons can be used to infer historical conditions such as cause of death and frequency and energy of post-mortem disturbance.

In the absence of physical disturbance, empty coronas can persist on the seafloor for months even in warm waters (more than 10 weeks for *Arbacia* in our 30°C experiments) and perhaps years under the right conditions (cold water; see observations by Ernst et al. 1973 of epifauna on fragile Recent endobenthic echinoids). This should provide ample time for infestations by encrusting and boring organisms.

Threshold Effects.—Collagenous ligaments

TABLE 2. Results of two-way ANOVA for effect of temperature and oxygen concentration on test strength and test toughness. Specimens held in different treatments for 4 weeks.

Source of variation	df	SS	MS	F
Test strength (Force)				
Temperature	2	18,386	9,193	42.5 ($P < 0.05$)
Oxygen	2	2,201	1,101	5.1 ns
Temperature*oxygen	3	2,843	948	4.4 ns
Test toughness (Work)				
Temperature	2	1,969	984	118.7 ($P < 0.01$)
Oxygen	2	149	74	8.9 ns
Temperature*oxygen	3	217	72	8.7 ns

that bind coronal plates require about two weeks to decay at 23°C. Carcasses allowed to decay beyond this threshold period all disintegrate at very rapid rates upon tumbling. Pre- and post-threshold carcasses also show a different pattern of disintegration. Breakup of fresh carcasses and those held at cool temperatures is largely by fracture across plates and requires considerable force or work, such as applied by test-crushing predators (Smith 1984), coarse debris thrown during storms (Strathmann 1981) or prolonged tumbling (this study). Coronas break by a combination of plate fracture and ligament failure during initial postmortem decay. After this threshold period of decay, carcasses break up much more quickly and easily by the ripping of weakened ligaments at plate sutures. These post-threshold carcasses have one-quarter or less the mean breaking strength of fresh carcasses and only rarely show cross-plate fractures; instead they yield a collection of unbroken, dissociated plates.

These results indicate that cross-plate fractures cannot be used to discriminate precisely between pre- and post-mortem breakage in fossil specimens (*contra* Schäfer 1972; Strathmann 1981; Smith 1984). Cross-plate fractures can be produced at any time up until the ligament decays, which takes two weeks for *Strongylocentrotus* at 23°C, but an unknown longer period in waters of 11°C or colder. On ecological and geological time scales, this period is still very short. The threshold effect introduces considerable ambiguity into the interpretation of cross-plate fractures in fossil specimens, since they can be produced taphonomically by processes completely unrelated to mortality.

Although fossil specimens consisting of disarticulated but closely associated plates and spines (state d of Smith 1984: p. 17; Schäfer 1972) suggest quiet water collapse of carcasses by ligamental decay, none of our quiet-water experiments produced this pattern within ten weeks. Our study suggests that, at least among strongylocentrotids and arachiids, this mode of preservation requires either very long exposure on the seafloor (perhaps with anoxic overlying waters to exclude scavengers and other organisms) or some triggering distur-

bance of the carcass not otherwise recorded in entombing sediments (see section on taxonomic differentiation).

Temperature Effects Are Much More Important Than Aeration.—By both semi-quantitative and quantitative measures, temperature has a dramatic effect on rates of organic decomposition: cool waters retard disintegration manyfold relative to room and warm waters, permitting intact coronas (\pm spines) to persist for a few months at minimum. In contrast, anoxia had no significant retarding effect in our experiments. Disarticulation of anaerobically decayed carcasses was as rapid as aerobic decay at all temperatures.

These results on the effects of oxygen corroborate Plotnick's (1986) finding that arthropods exposed to anaerobic decay disintegrated as rapidly as those undergoing aerobic decay under otherwise identical laboratory conditions. Our Winkler titrations from similar experimental setups suggest that Plotnick's aerated sediment-free tanks probably were in fact permitting aerobic decay, contrary to Allison's (1988: p. 151) concern that they were not. Thus, while we agree completely with Allison's (1988) finding that anoxia by itself is ineffective as a conserving medium, we differ with his implication that aerobic decay of carcasses proceeds significantly faster. We acknowledge that the interior of a carcass may well experience anaerobic decay even when surrounding waters are well aerated: decaying carcasses have a ferocious oxygen demand, obvious both stoichiometrically (Allison 1988) and circumstantially (e.g., halos of reduced sediment around many Recent and fossil carcasses, and rapidity at which non-aerated waters are depleted in experimental tanks). Our aerated experimental setups, however, should have allowed aerobic decay at least of the periphery of echinoid carcasses, especially the soft-tissue epithelium that covers the corona and spines. This should have measurably accelerated disintegration of the test if aerobic decomposition were significantly faster than anaerobiosis, but we observed no statistically detectable acceleration in any of our experiments.

The water in both aerated and sealed tanks

was not changed, and so dissolved metabolites (e.g., ammonium and organic exudates in both, hydrogen sulfide in anaerobic tanks) probably built up over the decay periods. Toxic metabolites should not have been more of a factor in one setup than in the other, however, since both setups received the same treatment. The scant evidence on metabolite production in the literature indicates in fact that dissolved organic carbon (one measure of exudates) builds up faster under anaerobic conditions than under aerobic conditions (Forree and McCarty 1970). However, carcasses in our aerated and sealed tanks showed no detectable difference in decay rates even when held at cold temperature (Fig. 6), where metabolites would be least likely to have been an inhibiting factor. We would thus go so far as to suggest, as did Plotnick (1986), that the effects of oxygen on decay are indistinguishable for macroinvertebrate carcasses.

This result is consistent with the rigorous laboratory studies of Westrich and Berner (1984), who demonstrated that anaerobic decay by sulfate reduction is a first-order reaction like aerobic decomposition and proceeds about as fast when supplied with the same quality of particulate organics. They found that anaerobic decay constants are 7.2 to 8.8/yr for fresh plankton (versus 7–26/yr if aerobic) and 0.44 to 1.02/yr for partially degraded plankton (versus 1.4 to 3.2/yr if aerobic). Based on a larger review, Canfield (1989) also found that oxic and anoxic (sulfate reduction) rates of decomposition are not significantly different when normalized for sedimentation rate, even under field conditions of mixed quality organics. The perception that sulfate reduction is slower or less efficient than aerobic decomposition stems from the fact that aerobic microbes exploit—and commonly deplete—labile organics first, leaving less metabolizable, refractory organics for the anaerobic microbial community to use. Under such conditions, sulfate reduction rates are retarded by the poor quality of organic material. Our observations (and those of Plotnick and Allison) that anoxia has scant inhibiting effect on the decay of macroinvertebrate carcasses suggest that, given a comparatively large mass of dead tissue rather than particulate

ulate matter, aerobic microbes deplete oxygen before they deplete all fresh organics. Thus supplied with fresh organics, anaerobic decomposition of the remaining carcass can proceed at a relatively fast rate until this reaction too is limited by oxidant supply or, alternatively, by early mineralization (*sensu* Allison 1988).

For proteinaceous skeletons, Allison (1988) found that the primary importance of anoxia as a conservation medium was not in retarding decay but in promoting early mineralization after initial decay. We did not specifically investigate early mineralization of echinoid tests, but Allison's experiments suggest that this could be practical on laboratory time scales. Certainly there is some potential for coronas to be stabilized very early in the post-mortem period either on the seafloor or when shallowly buried by: (1) "precocious" syntaxial overgrowths (Bromley 1979), particularly within highly porous stereom along plate sutures (Smith 1980); (2) stabilization of the high-Mg calcite tests by early diagenetic loss of magnesium on or close below the seafloor (e.g., as observed in Recent bryozoan debris; Nelson 1978; Nelson et al. 1988); and (3) mineralization of collagenous connective tissues by pyrite, calcite, or apatite, analogous to the early mineralization observed experimentally by Allison (1988) and inferred for many fossil specimens (Pinna 1985).

The primary role of anoxia in the preservation of articulated calcareous tests is probably in inhibiting scavengers. Even small-bodied scavengers (polychaetes, isopods) have a significant accelerating effect on the disarticulation of macrobenthic carcasses as demonstrated by caging experiments (Meyer 1971; Plotnick et al. 1988), although it is not known how significant this is relative to other factors. Anoxia of overlying waters and burial under a sufficient sediment blanket would both be effective, individually or in combination, in isolating carcasses from scavengers and thereby allowing decomposition to proceed according to the temperature- and decay time-dependent pathways described above.

Paleontologists rarely invoke low temperature to explain good preservation of articulated specimens: many cite anoxic waters and

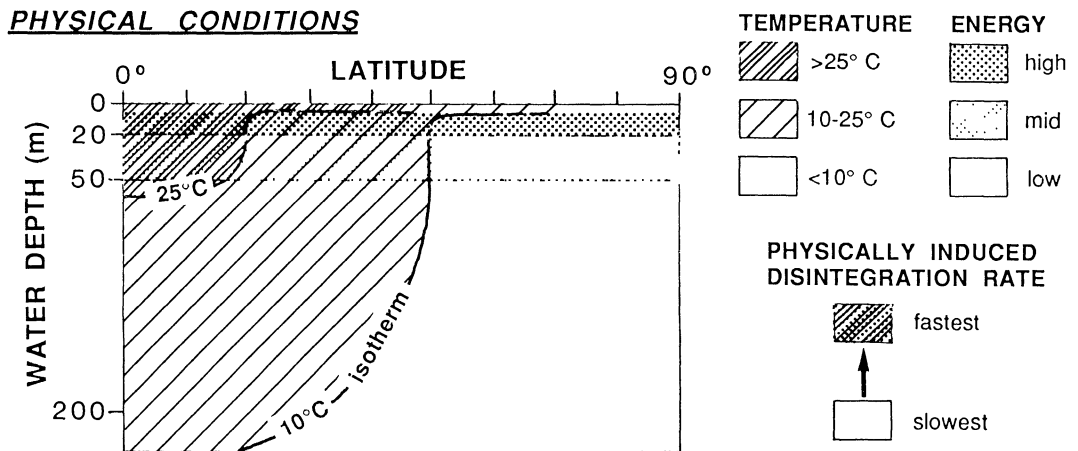


FIGURE 12. Variation in physical controls (temperature and water energy) on echinoid disintegration as a function of latitude and water depth, and expected effects on rates of disintegration. Isotherms are based on data in Sverdrup et al. (1942) and represent average positions for modern oceans; positions vary over 20° latitude seasonally and from east to west sides of major ocean gyres. The northern excursions of isotherms in the shallow water part of the graph indicate the elevated temperatures possible in small enclosed bodies of coastal water; in areas of free circulation, the entire upper 50 m of the water column is usually homogeneous in temperature. Depth zones of water energy are calibrated to sedimentary patterns in the modern North Sea (Aigner and Reineck 1982) and Texas continental shelf (unpubl. data).

smothering sediments. It is clear from our experiments as well as from those of Plotnick (1986) and Allison (1988) that anoxia in itself is not sufficient to explain good preservation. Anoxic porewaters theoretically should be no more effective than anoxic overlying waters. Moreover, from Plotnick's field experiments (1986; Plotnick et al. 1988) and from other observations it is also clear that burial does not improve preservation unless it is deep enough to sequester carcasses from bioturbators and erosional reworking. On aerated, actively bioturbated seafloors, the requisite thickness of burial deposits would range from 10–20 cm and up (callianassid shrimps commonly burrow to a meter or more), thus limiting the number of settings where rapid, deep, permanent burial is a likely mode of echinoid preservation. In warm water settings, a minimum depth of burial might also be necessary for carcasses to obtain sanctuary from temperature effects.

Although neither low temperature nor anoxia are sufficient in themselves to insure preservation of articulated skeletons, the combination would be an excellent means of delaying disintegration until permanent "deep" burial occurs. Alternatively, deep catastrophic burial (obrution; burial as the agent of mor-

talinity) is probably very effective by itself, but is generally invoked only where independent sedimentologic features point to storms, slumps or turbidity currents (Brett and Seilacher in press). Our experiments suggest that low temperature could enhance preservation of obrution Lagerstätten, as well as lengthen the period over which carcasses could persist intact before burial, and therefore should be considered along with anoxia as a potential contributing factor to the formation of these paleontological bonanzas. Echinodermal Konservat-Lagerstätten attributed to anoxia (stagnation) alone may bear reexamination in light of potential temperature effects (see reviews by Seilacher et al. 1985; Brett and Seilacher in press).

Predictions for the Fossil Record

Echinoid carcasses can be quite durable when fresh, and under cool and cold water conditions they can be maintained in fresh condition for at least a few months. This is a significant period of time, ecologically and taphonomically. Thus, although regular echinoids are undeniably fragile compared to many other superorders, classes, and phyla, a considerable range in states of preservation should be possible without truly extraordi-

PREDICTED PRESERVATION POTENTIAL

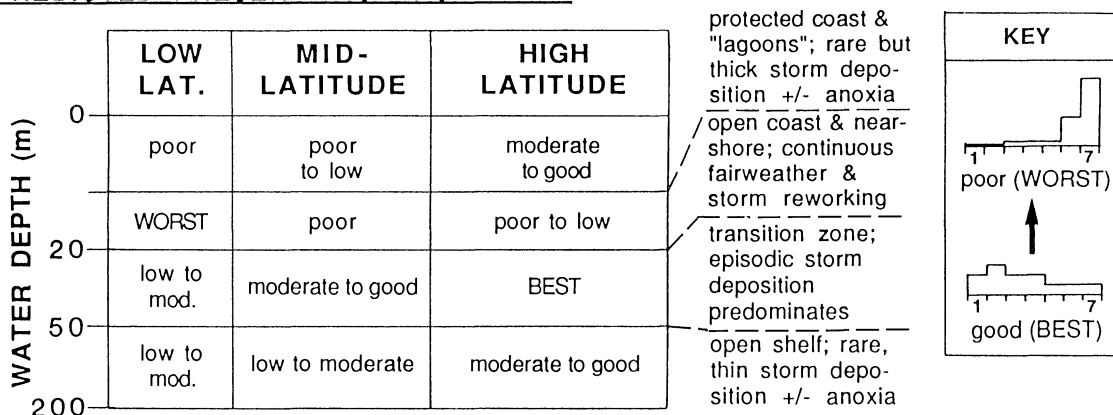


FIGURE 13. Quality of echinoid preservation is expected to improve from low to high latitudes within any single environment because of decreasing water temperature. The bathymetric gradient is more complex (i.e., non-monotonic) owing to the combined effects of temperature, water energy, and the frequency, thickness, and permanence of storm deposits. At any given latitude, preservation should be poorest in unprotected nearshore zones (above fairweather wavebase; specimens dominated by state 6 and 7 fragments, which may be size-sorted and abraded). The highest quality preservation should be found just offshore in the transition zone where storm deposition dominates rather than storm erosion and reworking (full range of preservation states with a significant number of specimens in states 1-3). Overall, the worst preservation should be in low-latitude nearshore facies and the best in high-latitude transition facies.

nary circumstances. The relative abundance of states of preservation should vary along environmental gradients for any given taxa: preservation should be poorest where temperatures and/or energy are highest (Figs. 12 and 13). In addition, taxa within any given fauna should differ in quality of preservation as a function of constructional details (Table 3).

Paleolatitudinal Gradients.—Time required for collagenous ligament decay ranges from

a few days at 30°C to something in excess of four weeks at 11°C under laboratory conditions. Because these temperature-dependent disintegration rates vary by at least an order of magnitude, there is potential for a paleolatitudinal gradient in preservation (Fig. 12). The "window for preservation" is very short in warm waters, and so carcasses in low latitudes should have the lowest probability of being entombed as taxonomically identifiable specimens (large coronal fragments or bet-

TABLE 3. Likelihood of good preservation based on how plates articulate at sutures. Data from Durham et al. (1966), Kier (1977), Régis (1977, 1979), and Smith (1980, 1984). ? = uncertain construction. Boldface = regular echinoid group known from the British Upper Chalk.

Higher Preservation Potential Expected →			
Flexible corona	Rigid corona (collagen fibers penetrate plate stereom)		
Imbricated plates, embedded in non-penetrating collagen	No or rare interlocking of stereom, plates abut or bevel	Limited interlocking of stereom (pegs & pits)	Extensive interlocking (hooks or deeply penetrating needles)
Echinocystitoida Pz Cidaroida Echinothurioida some Diadematoidea (especially Diadematidae & Micropygidae)	Bothriocidaroida Palaechinoida post-Tr Cidaroida some Diadematoidea Pedinoida Pygasteroida Heterocidaridae ? Plesiocidaroida	Hemicidaroida Arbacioida Temnopleuroidea Echinoida (includes <i>Strongylocentrotus</i>) ? Salenioida ? Phymosomatoida ? thin-walled irregulars (non-clypeasteroids)	Clypeasteroida
		↙ ? Orthopsida ↘	

ter). Carcasses in high latitudes should have the greatest probability. These conclusions are supported by the field experiments of Greenstein (1989a), who found that in warm water, near-reef environments of the Bahamas and U.S. Virgin Islands, regular echinoids lost their spines in 6 days and broke into large or small fragments in 12 days; identifiable specimens were rarely found with live individuals.

Assuming that test-crushing predators, scavengers, and bioturbators do not have a disproportionate effect in high versus low latitudes, temperature effects would translate into fossil faunas having different proportions of well and poorly preserved specimens (Fig. 13). This would have immediate implications for diversity studies. Firstly, high latitude fossil assemblages would approximate original faunal diversity more accurately than low latitude assemblages. Secondly, Recent species diversity for regular echinoids is highest in the tropics and this trend persists back through the record (Smith 1984: p. 124). If a gradient in preservation potential exists, then paleontological estimates of diversity gradients are conservative with respect to tropical maxima. Paleontological estimates are even more conservative if predation in general is more intense in low latitudes than in high latitudes (Vermeij 1978).

A taphonomic gradient would also bias estimates of the importance of predation in fossil echinoid faunas. Because pre-threshold carcasses can fracture like live echinoids, cross-plate fractures in cold-water death assemblages are more ambiguous than in warm-water assemblages because the threshold period is longer. In warm-water settings where ligaments decay rapidly, cross-plate breaks can be interpreted as mortality-related with much greater confidence than in cold-water settings.

If a latitudinal gradient does exist (Fig. 13), taphonomic analysis of echinoids might become a useful corroborating method of paleoclimatic interpretation.

Paleobathymetric Gradient.—A depth-related gradient in preservational quality is also possible owing to the combined effects of temperature, water energy, and depositional

events. However, this gradient probably is *not* monotonic, because not all physical factors vary monotonically (Figs. 12 and 13).

The poorest preservation at any latitude is expected in beach and nearshore zones above fairweather wavebase, where carcasses on and shallowly buried beneath the seafloor have the highest likelihood of physical reworking. Even carcasses protected initially by catastrophic burial (oburbation) are likely to be broken up and dispersed before final entombment. These intertidal to shallow subtidal settings are characterized by rocky shore, beach, and amalgamated storm sands (Aigner 1985; Miller et al. 1988; Brett and Seilacher in press), where isolated or broken plates and spines, locally size-sorted into lags and/or heavily abraded, should typify echinoid remains. All else being equal, nearshore zones at high latitudes might have marginally better preservation than at low latitudes.

Lee settings—back-barrier lagoons, protected stretches of coastline, intertidal flats—should be characterized by slightly better preservation. Although such sites can have anomalously high temperatures for their latitude and thus accelerated disintegration rates, such settings also experience episodes of rapid, thick sedimentation in the form of flood deposits, beach washovers, and tidal surge during above-average storms. By excluding scavengers, such events and longer periods of anoxia would also favor better preservation from time to time relative to the beach and nearshore of less protected coasts. Thus a significant proportion of whole coronas or large coronal fragments, both from local and transported populations, should be expected along with dissociated plates and spines (e.g., "lagoonal" examples of Bantz [1969] and Seilacher et al. [1985]).

The best preservation is expected in transition-zone environments. This zone lies below fairweather wavebase and above the wavebase of average storms and, in contrast to the nearshore zone of storm erosion and redeposition of sediment, is dominated primarily by storm *deposition*. In the modern Helgoland Bight (North Sea; Aigner and Reineck 1982) and Texas continental shelf (Gulf of Mexico; unpubl. data) the transition zone lies

between about 20 and 50 m water depth; these values were used to calibrate Figs. 12 and 13. Compared with the nearshore zone, obrution specimens in the transition zone are less likely to be reworked physically (because of dampened wave energies) or biologically (because of relative thickness of storm deposits). Aslin (1968) described an excellent Bathonian example of such a facies: in slump-event deposits of muddy limestone, *Acrosalenia* occurs as intact, spine-bearing specimens (state 1), whereas in background well-sorted fragmental limestone deposits, it occurs only as abraded coronas and fragments (states 4 through 7). This range of states of preservation suggests deposition in the shallow range of storm-reworking. Quality of preservation within the transition zone should deteriorate from best in high latitudes to only moderately good in low latitudes: disintegration rates in warm waters are still fast relative to the frequency of storm depositional events, even in this otherwise most favorable of sedimentary environments. Catastrophic storm deposition, in which burial is also the agent of mortality, may show no such latitudinal variation.

Offshore of the transition zone, in deeper open-shelf environments below average storm wavebase, the expected quality of regular echinoid preservation decreases (Fig. 13). Storm deposits are typically rarer and thinner and thus should be less effective in protecting carcasses from biological disturbance; fewer well-preserved specimens (i.e., states 1-3 or 4) are expected. Episodes of anoxia could counteract the effects of post-mortem exposure on the seafloor, so here, as in most settings, a range of possible preservation states is possible. High-latitude open shelves should be characterized by better preservation, on average, than mid- and low-latitude open shelves. The latter two should differ little from each other owing to similar temperature regimes (Fig. 12).

To summarize, we expect regular echinoid preservation to be determined qualitatively by the immediacy, thickness, and permanence of burial. Water temperature and oxygenation of overlying waters determine exactly how immediate and deep that burial must be to effectively sequester carcasses from

taphonomic damage. Because transition-zone depths are likely to have the best quality preservation, these tempestite-dominated facies should yield disproportionately diverse faunas and a disproportionate number of first occurrence datums, since taxonomists rarely choose to define new taxa using isolated plates or spines alone.

Taxonomic Differentiation.—Test construction should influence the preservation of echinoid groups (Kier 1977; Smith 1984), but our experiments suggest that different aspects govern the disintegration of fresh (pre-threshold) and decayed (post-threshold) carcasses on the seafloor.

Because coronas of fresh carcasses (and of live specimens; Strathmann 1981) break preferentially across plates rather than along plate sutures, collagenous bindings are clearly stronger than the calcitic stereom. Thus extensive interlocking of stereom across plate sutures should not provide any particular preservational advantage to a group during the pre-threshold period when collagenous tissue is intact. Differential preservation of echinoid groups in the pre-threshold period must be controlled by other aspects of test construction.

The most likely controls include factors that permit echinoids to withstand physical damage while alive, i.e., coronas composed of plates of high individual strength (either thicker plates or some particular stereom type?), and sturdy spines. These effects are measurable even between the two species of the genus *Strongylocentrotus* that we investigated, and are likely to be even more pronounced among regular echinoid groups at higher taxonomic levels. Strathmann (1981), for example, found that strength to impact of live echinoids decreased from the club-spined *Eucidaris* to the progressively weaker spined *Echinometra*, *Diadema*, and *Tripneustes*.

Among post-threshold carcasses, the extent of stereom interlocking becomes more important in preventing disintegration of coronas since collagenous connective tissues have decayed (Table 3). Echinoids with imbricate plates embedded in soft tissue (many Paleozoic forms; post-Paleozoic echinothurioids; some diadematoids) should be most prone to

post-threshold disarticulation (collapse should require little or no physical agitation), followed by other diadematooids and cidaroids whose plates abut or bevel at sutures and are penetrated by connective ligaments but generally lack interlocking stereom, and finally an array of echinaceans whose plates have microsinuous, peg-and-socket sutures (Régis 1977, 1979; Smith 1980, 1984; Table 3). The coronal plates of irregular echinoids interlock to a much greater extent than those of most regular echinoids, culminating with the deeply interpenetrating stereom needles of some clypeasteroids (Seilacher 1979; Smith 1984). The minimum strength of post-threshold carcasses having interlocking stereom thus should approximate or equal the strength of individual plates, significantly improving the preservation potential of such taxa.

The influence of test rigidity on echinoid preservation (Smith 1984) is borne out by our post-threshold decay experiments and anecdotal information from Recent environments. Kier (1977), for example, mentioned that in 15 years he had never found an intact dead *Diadema antillarum* even though this is the most common of all Caribbean echinoids. Moreover, in the course of burial experiments he found that only *Clypeaster rosaceus* survived three months without disarticulation, in contrast to the regular echinoids *Eucidaris*, *Diadema*, *Lytechnis*, and *Tripneustes* (latter two are Temnopleuroidea), and thin-walled irregular echinoids *Meoma*, *Paraster*, and *Cassidulus*. Both Smith (1984) and Seilacher (1979) have noted that clypeasteroids are the only group to form coquinas and thus apparently the only group consistently able to survive exhumation, reworking, and possibly some transport. Irregular echinoids are also far more frequently found encrusted and bored than regular echinoids (Ernst 1966; Ernst et al. 1973). Finally, in a recent series of definitive experiments, Greenstein (1989a) was able to quantify the influence of test construction using bleached carcasses: *Diadema* degrade within a few minutes of tumbling, and *Tripneustes* and *Eucidaris* degrade within a few hours, whereas *Echinometra* (Echinoidea) survives more than 100 hours of laboratory tumbling.

Ecological Factors.—The patterns we can ex-

pect in the fossil record will also be influenced by such ecological factors as mode of death, relative activity of scavengers, and taxonomic differences in palatability. The persistence of coronas in the warm-water backreef lagoon of Discovery Bay, Jamaica, for example, may owe in part to overfishing, which would reduce the likelihood both of predation and post-mortem disruption in this quiet-water setting; encrusting organisms might actually strengthen the corona against post-threshold collapse. Intact coronas found on the deep forereef, by contrast, must reflect the combined effects of low temperature and of less abundant or less opportunistic scavengers. Predators that pluck out internal soft tissues may actually enhance preservation of coronas by reducing the carcass's attractiveness to scavengers, as suggested by Ernst et al. (1973). Gradients in the abundance of coronas (state 4) therefore may in part reflect gradients in method of predation. Certainly our studies suggest that if coronas can escape major damage during death, they can persist for considerable periods without taphonomic damage other than spine loss.

Preservation of Fossil Echinoids: A Preliminary Test Using Upper Cretaceous British Chalk Species

Excluding examples that consisted of spines only, we tabulated the preservation state of all regular echinoid specimens identified to species level in the extensive white chalk facies collections of the Natural History Museum, London. These specimens totalled 804 individuals and 25 species and include late Turonian to Campanian (*Sternotaxis plana* through *Belemnitella mucronata* zones) representatives of the Cidaroida, Echinothuriacea, Diadematacea, and Echinacea (Salenioidea and Phymosomatoida).

Our aims were to determine whether experimental stages in carcass disintegration could be recognized; whether fossil taxa underwent the same sequence of disintegration; whether differences in test construction were expressed as preservational differences; and whether fossil coronas exhibited evidence of seafloor exposure, such as borings and encrustation. Ideally, our predictions for preservation should be tested using newly col-

lected material, so that biases could be reduced or at least made consistent. This was not practical for a pilot study because of the great rarity of regular echinoid specimens (see Kier 1977 for typical numbers of specimens per genus and family).

The extensive and well-curated regular echinoid collections of the Natural History Museum (NHM), accumulated over several centuries but recently updated taxonomically by Smith and Wright (1989; in press), presented a reasonable compromise where variation in quality of preservation might be determined for large samples. Because spines are often removed by air-abrasion preparation to reveal taxonomically important features of the corona, we are somewhat suspicious of interpreting data on the relative abundance of preservational states. It also appears that curation biases *against* superbly preserved specimens by our scale, favoring spineless state 3 and 4 conditions; state 6 and 7 specimens are also less likely to be collected and curated if state 3 and 4 specimens are abundant. If our survey yielded sensible patterns, notwithstanding known limitations of museum collections, then more laborious testing and applications in the field would be justified.

The Upper Cretaceous Upper Chalk of Britain records a mid-latitude, deep-water shelf setting (80–300 m; Hancock 1975; Hakansson et al. 1974) where a large array of preservational states should be possible. Although white chalk facies may superficially appear to be lithologically homogeneous, they exhibit considerable bed-by-bed variation and reflect a range of subenvironments and episodic events (Hancock 1975; Kennedy and Garrison 1975; Mortimore 1986). The zone-level (and poorer) stratigraphic resolution possible with museum collections is much coarser than this lithologic variation and consequently some perceived variation in quality of preservation of species may relate to small-scale differences in taphonomic conditions. A fuller treatment of these data along with our presently unpublished data for regular echinoids from other museum collections and Upper Cretaceous facies will appear elsewhere.

Results.—All seven stages of disintegration (Figs. 1 and 2) could be identified within or

among Upper Chalk species (Fig. 14, a–d). As a consequence of the survey, we found it useful to distinguish an additional category—state 4a—for empty coronas with apical plates intact. We also indicated by a + or – whether state 3–6 specimens still had attached spines.

The multiple states of preservation recognized within species suggests that Cretaceous carcasses disintegrated in the same basic sequence as did our experimental carcasses. For example, species preserved as well as state 1 were also represented by specimens in states 2–7; those whose best preservation was state 2 also occurred in states 3–7; etc. (Fig. 15). Empty coronas (state 4) and large coronal fragments (state 6, usually consisting of coronal segments detached along amb-interamb sutures) were the most commonly encountered modes of preservation. The only notable departure was the abundance among cidaroids of empty state 4 coronas with attached spines (up to 37%; Fig. 14, c). These indicate either especially strong spine attachment (i.e., stronger than attachments for lantern) or “early removal” of lanterns by predators. Another notable pattern was the rarity of damaged but intact coronas (state 5; Fig. 15). In our lab experiments, only fresh carcasses persisted in this state during tumbling; post-threshold specimens rapidly went from state 4 to state 6. The rarity of fossil specimens in state 5 thus might be a meaningful reflection of the comparatively low-energy chalk setting.

Differences in quality of preservation suggest that echinoid taxa disintegrate at different rates. Preservational envelopes for the eighteen most common Upper Chalk species in the NHM collections are shown as normalized histograms in Fig. 15, where they are arrayed in rank order (note that ranking is unrelated to sample size). The cidaroids *Tylocidaris* and *Temnocidaris* (*Stereocidaris*) attain the highest quality of preservation (state 1 and 2, respectively), implying greatest resistance to disintegration. *Hirudocidaris* and three phymosomatoids achieve the next rank (best preservation = state 3), followed by two more cidaroids, all five Upper Chalk salenioid species, a phymosomatoid (*Gauthieria*), and a temnopleuroid (*Boletechinus*) (best preservation = state 4 or 4a). Finally, the diadematiid *Cen-*

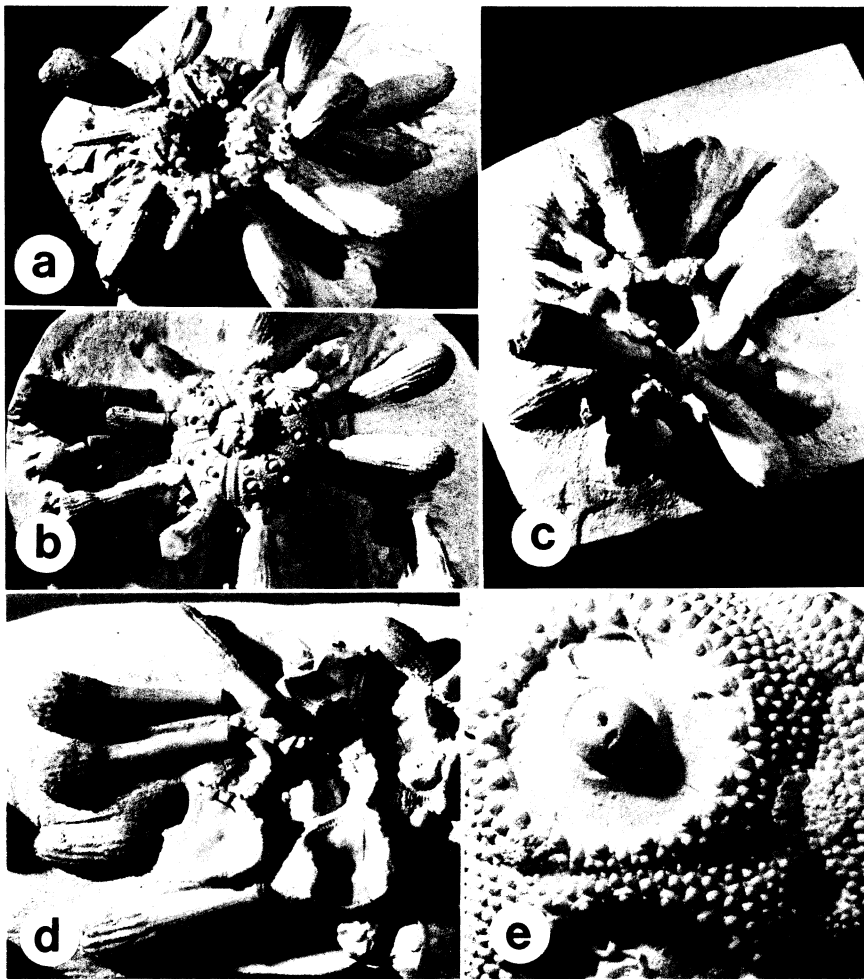


FIGURE 14. Upper Cretaceous cidaroids from the Upper Chalk of Britain show a full range of states of preservation. *Tylocidaris clavigera* in (a) state 1 (NHM specimen E57578), (b) state 2 or 3 (E39998), (c) state 4 with attached primary spines (E75562; may indicate predation), and (d) state 6 with closely associated spines (E27565). (e) Fouling organisms on *Hirudocidaris hirudo* (E39813) indicates post-mortem persistence of the intact corona on the seafloor for one or more seasons: acrothoracican barnacle boring on tubercle mamelon; period bivalve *Atreta nilssoni*, serpulids and encrusting forams on tubercle aeroles; bryozoan colonies span plate sutures (E39813).

trostephanus and echinothurioid *Echinothuria* exhibit the poorest "best" states of preservation (state 6), suggesting least resistance to disarticulation under the same suite of Upper Chalk conditions.

This ranking accords fairly well but not precisely with known differences in test construction (Table 3). First, as befits their poorly articulated tests, the diadematids and echinothuriids show the poorest preservation. This ranking is not an artifact of small samples. According to Smith and Wright (in press), *Centrostephanus fragile* is the *only* fossil dia-

dematoid known from material other than isolated spines, and *Echinothuria floris* is one of only three fossil echinothuriids in the world known from more than isolated spines. The NHM specimens, although few, thus define the upper limit of preservational quality for these two groups.

Secondly, members of Echinacea (represented by *Salenia*, *Phymosoma*, *Gauthieria*, and *Boletechinus*) all show a similar range in quality of preservation within the Upper Chalk (predominately state 4, rare state 3 specimens; Fig. 15). It may be meaningful that, in the

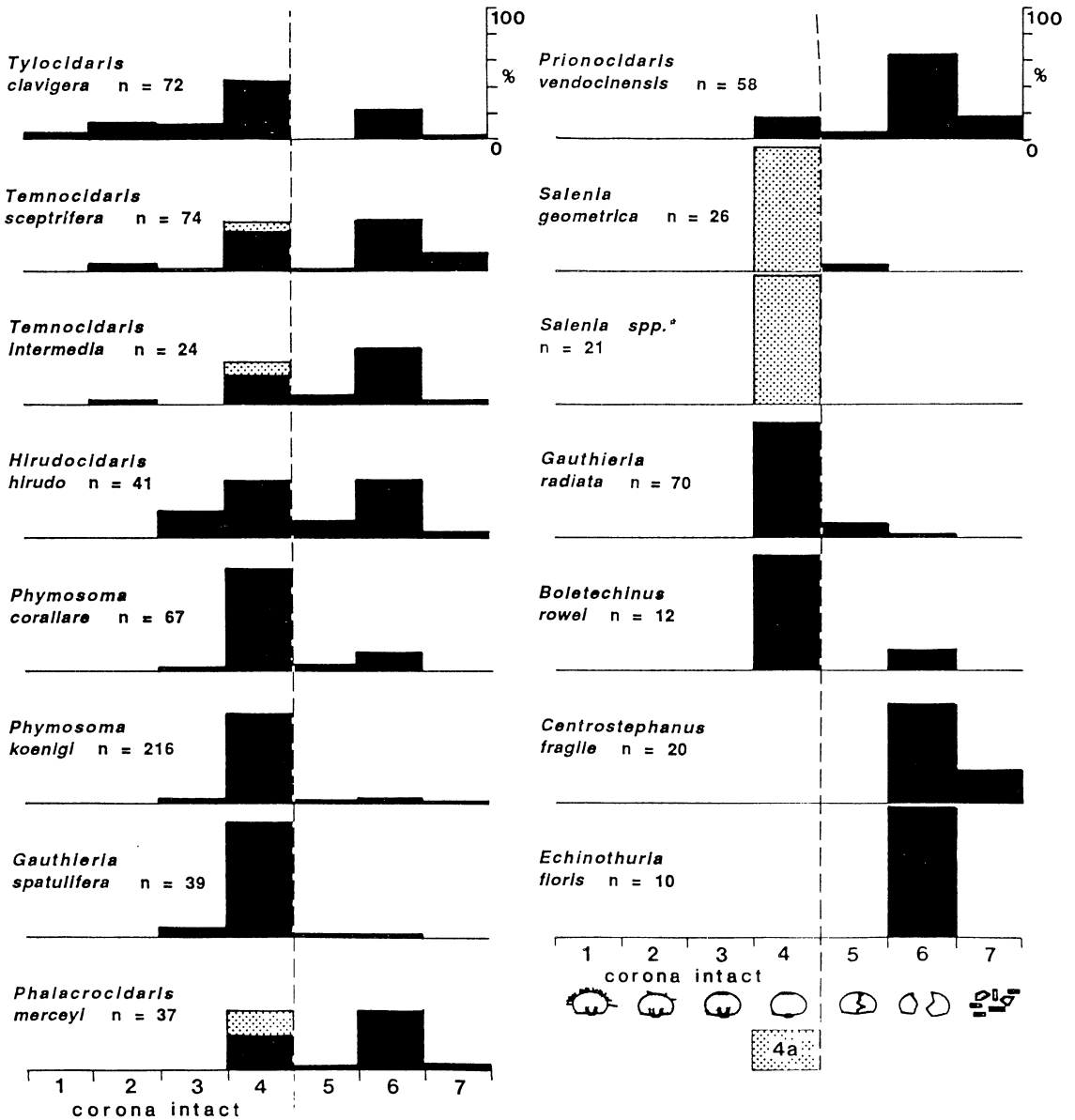


FIGURE 15. Preservational quality of British Upper Chalk echinoids from the Natural History Museum, ranked from best (*Tylocidaris clavigera*) to worst (*Centrostephanus fragile* and *Echinothuria floris*), normalized to 100%. State 4a (stippled) designates empty coronas with intact apical systems. n = number of specimens.

absence of physical disturbance, experimental *Strongylocentrotus* also became "stuck" in states 3 and 4 in lab experiments. Alternatively, these museum data may only indicate that state 6 and 7 specimens were not collected or identifiable taxonomically.

The cidaroids, expected to have a preservational envelope intermediate to the echinaceans and the diademataceans and echino-

thuriaceans, show no consistent pattern (Fig. 15). This variation among cidaroid species may reflect differences in microhabitat, ability to escape anastrophic burial, palatability to "gut-plucking" predators, or some other ecological factor. Alternatively, the unexpectedly good preservation of cidaroids relative to echinaceans might be due to heavier connective ligaments between plates. These could conceiv-

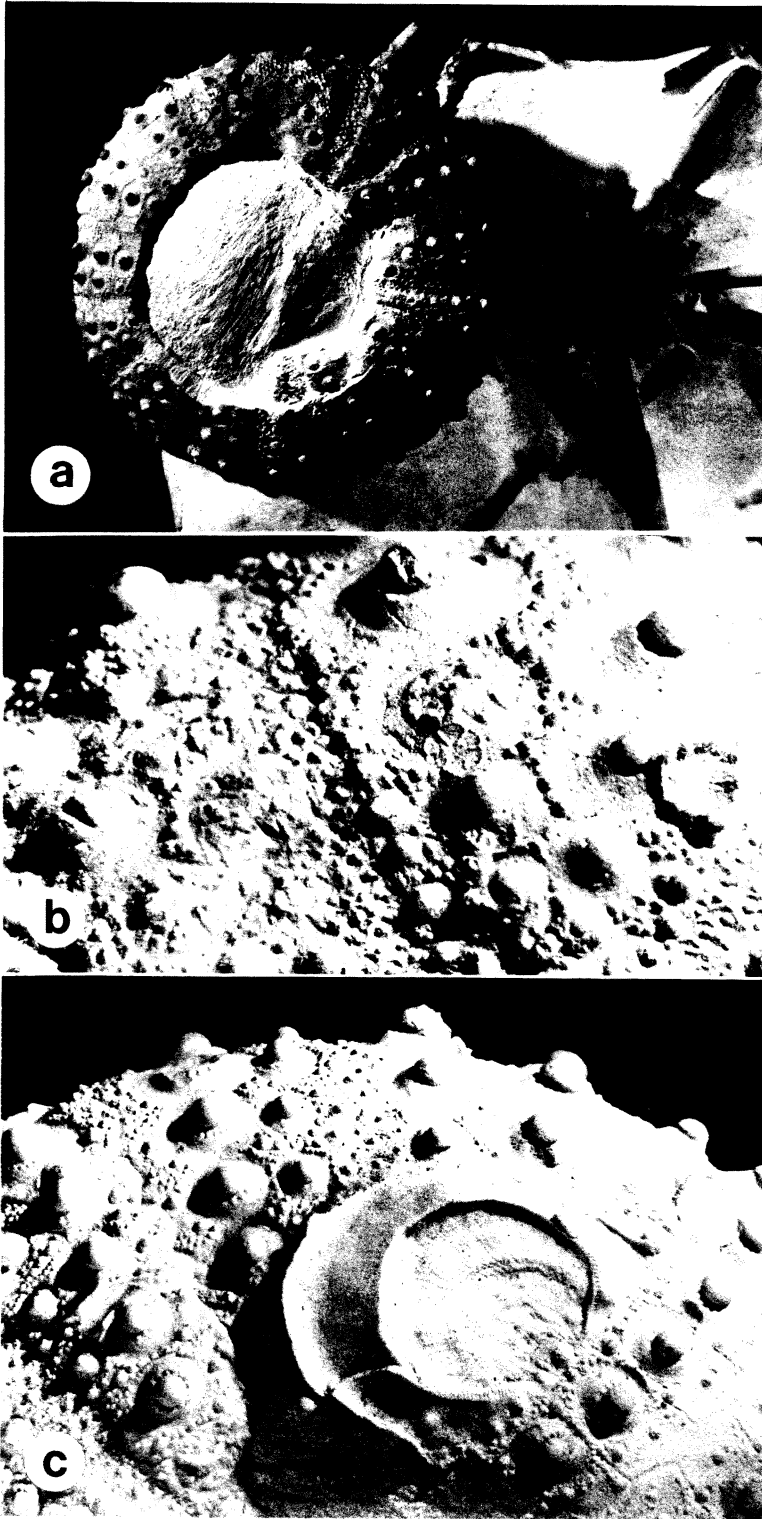


FIGURE 16. Probable post-mortem infestations of Upper Chalk phymosomatids (Echinacea). a, encrusting bryozoans on empty corona of *Phymosoma koenigi* (E76001); b, septate base of solitary coral (center), concave ventral valve of thecidean brachiopod (right), acrothoracican barnacle boring on tubercle mamelon (left), and star-shaped *Gnathichnus* (echinoid grazing traces, left) all on oral surface of *P. sp.* (E17160); c, large and small specimens of *Atreta nilssoni*, worn serpulid tube (left), and other small encrusters on apical surface and ambitus of *P. sp.* (E17142).

ably prolong the pre-threshold period, compensating for the lack of interlocking stereom.

The presence of boring and encrusting organisms on empty coronas provide further evidence for the post-mortem persistence of echinoids on the chalk seafloor (Figs. 14, e and 16). Encrusters on regular echinoids are almost always small and include several kinds of sheet and branching bryozoans, the pteriod bivalve *Atreta*, sclerosponges, several kinds of serpulids, encrusting foraminifers, thecidean brachiopods, spirorbids, and a possible solitary coral. Borings appear to be limited to those produced by acrothoracican barnacles, which preferentially attacked mamelons (tips of tubercles). Noting that perforations on regular echinoids are rare, de Saint-Seine (1951) also observed acrothoracican borings on Cretaceous cidaroid tubercles.

Fouling organisms were most frequent on phymosomatids, suggesting that their coronas were particularly sturdy despite a thin-walled construction. *Hirudocidaris hirudo* was the only other echinoid that carried this fauna (Fig. 16, e). Foulers were found exclusively on specimens in states 4–6, but it is possible that some had commensal relationships to the echinoids. Further study of Recent and ancient, regular and irregular echinoids is needed to determine how many of these associations are strictly taphonomic in nature.

Conclusions

Experimental taphonomy quantifies the relative fragility of regular echinoids under a range of physical conditions and yields several new applications and caveats to paleoecological and paleoenvironmental interpretation.

1. Under laboratory conditions, regular echinoids disintegrate in a systematic sequence. Deviations from this sequence occur among fresh carcasses and carcasses held at low temperature—their coronas typically fracture before the lantern and all spines are lost—and as a consequence of some kinds of predation (removal of lantern, resulting in empty coronas with spines still attached).

2. Rates of disintegration by physical agitation are directly influenced by the period of initial decay. Consequently, state of pres-

ervation is not necessarily a good indicator of environmental energy or distance of transport, as also found by Allison (1986) for proteinaceous and soft-bodied macrofauna.

3. Both rates and styles of disintegration show a threshold effect related to decay-weakening of collagenous ligaments. Cross-plate fractures thus are uncertain indicators of traumatic death (predation, storm thrashing), since they can be post-mortem in origin. Threshold effects should be minimized for echinoids having extensive stereom interlocking at plate sutures (e.g., the irregular clypeasteroids).

4. Rates of decay are slowed significantly by low water temperature, suggesting the potential for a strong latitudinal gradient in quality (and quantity) of echinoid preservation.

5. Low temperatures are far more effective inhibitors of decay than anoxia, whose primary influence on the preservation of multi-element calcareous skeletons may be to exclude scavengers. Echinodermal Lagerstätten attributed solely to obrution and/or stagnation may bear reconsideration in this light.

6. The combined effects of physical agitation and temperature also suggest the potential for a detectable bathymetric gradient in preservation that would be superimposed on latitudinal gradients. At any given latitude, preservation should be best in storm-influenced transition zones (below fairweather wavebase, dominated by storm deposition) and worst in the nearshore to beach zone (and other above-fairweather wavebase shoals) where sediment reworking is most intensive.

7. As suggested by others, taxonomic differences in test rigidity related to sutural interlocking should cause differential preservation of echinoid groups (Table 3) and this is borne out by our survey of an Upper Cretaceous fauna. Our experiments indicate that such differences should only become detectable among post-threshold carcasses, because among pre-threshold carcasses it is connective tissue rather than stereom strength that keeps the test intact. Diversity and relative abundance measures based on echinoid death assemblages should thus be more biased in higher temperature than in lower tempera-

ture settings, and this bias should be taxonomically predictable.

Several of these observations—particularly regarding the significance of temperature in decay, and the differential behavior of pre- and post-threshold carcasses—should apply to the preservation of other organisms with collagen-bound, multiple-element skeletons. The existence of a decay-related threshold in the breakup of echinoid carcasses also underscores the pitfalls of assuming constant rates and/or linear models of taphonomic modification. Comparatively long-term experiments, such as described here, illustrate the likely complexity of post-mortem processes even under “abiogenic” laboratory conditions, and thus the dangers of extrapolating from short-term taphonomic observations. The presence of diverse endo- and epibionts on coronas provides a more specific caution that, although regular echinoids certainly are more fragile than many other invertebrate phyla including some other members of Echinodermata, they can persist over sufficient post-mortem periods to figure in ecological and sedimentological processes. Pathways from death to grave, even for regular echinoids, can be long and complex.

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