Evaluation of sand grain crushing in the sand dollar *Mellita tenuis* (Echinoidea: Echinodermata)

Roberta C. Challener^{1,2,*}, Molly F. Miller¹, David J. Furbish¹, James McClintock²

¹Earth and Environmental Sciences Department, Vanderbilt University, VU Station B Box 351805, 2301 Vanderbilt Place, Nashville, Tennessee 37235-1805, USA

²Department of Biology, University of Alabama at Birmingham, Birmingham, Alabama 35294-1170, USA

ABSTRACT: Sand dollars in the genus *Mellita* have been postulated to use their teeth to crush sediments comprised of quartz. If so, sand dollars may have a greater impact on nearshore siliciclastic environments than generally thought. The present study compared the size distributions of quartz grains in the guts and immediate habitat of the common sand dollar *Mellita tenuis* in summer and winter in Port Saint Joseph Bay, Florida. In both seasons, sand dollars had significantly greater frequencies of the smaller size classes of grains in their guts. The hypothesis that sand dollars crushed quartz sand grains with their teeth was evaluated using light microscopy. We compared the degree of angularity of ingested grains with those collected from surrounding sediments. Among 6 individuals examined (3 in summer and 3 in winter), only half (2 in summer and 1 in winter) had guts containing more angular grains than those in the surrounding sediments. A comparison of more angular grains isolated from sand dollar guts with artificially broken grains using scanning electron microscopy indicated that gut-derived grains lacked freshly broken surfaces. In a laboratory study, after 72 h of feeding upon quartz sediments with the smallest size classes (<250 µm) removed, sand dollar guts were full but contained only trace amounts of sediments <250 µm. We conclude that the smaller size classes of grains found in the guts of *M. tenuis* are not the result of grain breakage. Rather, grains are selected pre- or post-ingestion, perhaps to optimize the surface to volume ratio of particles so as to maximize ingestion of microbial films that coat sand grains.

KEY WORDS: *Mellita tenuis* · Sediment size selection · Quartz · Irregular echinoid · Benthic ecology

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INTRODUCTION

Sand dollars consume large amounts of sediment during feeding activities, and species that inhabit carbonate-rich substrates are known to pulverize the carbonate sands they ingest (Telford & Mooi 1986, Telford et al. 1987). It is also suggested that at least one species that occupies quartz-rich (siliciclastic) sediments, *Mellita isometra*, alters the size of quartz grains during feeding by crushing grains with the teeth associated with a modified Aristotle's lantern (Telford et al. 1985). If grain crushing is occurring to the extent described, then these sand dollars have a greater impact on nearshore substrates than previously thought, given the abundance and widespread distribution of

many species in siliciclastic substrates (Birkeland & Chia 1971, Stanley & James 1971, Ghiold & Hoffman 1986, Mooi & Harold 1994, Takeda 2008).

Quartz is both harder and more chemically stable than calcium carbonate (Walther 2005); the differences in tensile strengths between the teeth of echinoids and that of natural quartz is 4 orders of magnitude and thus it is highly improbable that sand dollar teeth are capable of breaking quartz grains. Echinoid teeth have a material hardness equivalent to fluorite (Klinger & Lawrence 1985); the tensile strength of fluorite is 0.1397 kg cm⁻² (Kukleva & Lodygin 1982), versus 1380 kg cm⁻² for natural quartz (Bechmann & Parsons 1952). Telford et al. (1985) suggested that there are inherent weaknesses (fracture planes) in quartz grains to

*Email: rchallen@uab.edu

explain how sand dollars may crush them; however, it is unlikely that such weaknesses in the grains reduce their tensile strength by 4 orders of magnitude. In addition, there are several hypotheses that suggest that the strength of a material, when measured per unit size, increases with decreasing size (Epstein 1948 and references within). Thus, although a very small percentage of quartz grains may contain sufficient flaws to facilitate breakage when grains are abraded against each other, it is unlikely that sand dollar teeth are breaking a significant number of grains during feeding.

The presence of sharp, highly angular particles within the gut of *Mellita isometra* (formerly *M. quinquesperforata*, Harold & Telford 1990) that were smaller than particles found in the food grooves of the sand dollar or the substrate were interpreted as further evidence for the alteration of grain size during ingestion (Telford et al. 1985). Yet particles in the surrounding substrate that are less than 50 μm in length are typically more angular than larger particles because they have both lower inertia and momentum, and particle rounding due to breakage is less likely to occur (Leeder 1982). Therefore, explicitly attributing higher grain angularity to the crushing action of sand dollar teeth during feeding could be problematic. A more detailed comparison of the surfaces of grains collected from natural substrate and from sand dollar guts utilizing scanning electron microscopy (SEM) may help to confirm the source of a grain's angularity.

The sand dollar *Mellita tenuis* (formerly *M. quinquesperforata*, Harold & Telford 1990) is a conspicuous member of sandy benthic communities ranging throughout the eastern Gulf of Mexico. They occur in densities of 1 to 17 and 7 to 114 ind. m^{-2} in nearshore (120 m from the shoreline) and offshore (120 to 250 m from the shoreline) environments, respectively (Lane & Lawrence 1980). Feeding behaviors other than sediment size preference (Pomory et al. 1995) have not been documented for *M. tenuis*, but a study with the closely related *M. isometra* from siliciclastic sediments along the central and southern Atlantic coast indicate they likely ingest quartz sediments using specialized podia that are particularly abundant on the oral surface of the test (Telford et al. 1985). Sediment grains are handled by podia covered in mucus (secreted at the tips of the podia), such that by the time the grains line the oral food grooves they are entrapped in mucus-bound cords. Facilitated further by a variety of podia, the mucus cords are then transported to the mouth (Telford et al. 1985). *M. isometra* uses the 5 teeth in its modified (flattened) Aristotle's lantern to scrape organic material from the surface of sand grains and the teeth may also break open diatom frustules to expose the cell contents to digestive enzymes. Telford et al. (1985) further proposed that, based on broken

frustules and small angular sediment particles observed in their guts, this species was capable of fracturing, fragmenting and thus crushing sand grains with its teeth.

The overall objective of the present study was to further evaluate whether representatives of the genus *Mellita* are indeed capable of crushing quartz sand grains during ingestion and thus altering nearshore sediment textures. We selected *M. tenuis* because it is a common inhabitant of the eastern Gulf of Mexico and a close relative of *M. isometra*. To evaluate this hypothesis we (1) compared the size classes of sediments in the guts of *M. tenuis* with those in the surrounding sediments; (2) employed light microscopy to quantify and compare the degree of grain angularity of individual grains removed from guts with those from the surrounding sediments; (3) used SEM to compare grain surfaces of artificially broken quartz grains with grains removed from sand dollar guts; and (4) conducted a controlled laboratory experiment to evaluate whether sand dollars presented only size classes of quartz grains $>250 \mu\text{m}$ possessed grain size classes $<250 \mu\text{m}$ in their guts following 3 d of feeding (i.e. they had crushed grains with their teeth during ingestion).

MATERIALS AND METHODS

Adult sand dollars (6.5 to 10.1 cm diameter) were collected by hand in summer (August 2007) and winter (December 2007) from Saint Joseph Bay on the panhandle of Florida. The collecting site was located at Eagle Harbor on the bay side of Cape San Blas (29° 45' 52" N, 85° 24' 7" W). Sand dollars were immediately turned onto their oral surfaces following removal from seawater, rinsed in seawater to remove exterior sand, and silicone caulking was placed over the mouth and anus to ensure sediments were not subsequently ejected. At the time of each sand dollar collection, sediment samples were collected using a 1.9 cm diameter, 5 cm length core (PVC pipe) from the same location (within 10 to 15 cm of the sand dollar collection site). Sand dollars were then euthanized in a solution of 25% magnesium chloride, stored individually in Ziploc® bags, placed in a cooler on ice and transported along with the sediment samples immediately to Vanderbilt University, Nashville, TN, where they were stored frozen at -20°C prior to subsequent analysis.

For each of the summer and winter collections, 3 adult sand dollars were thawed and their intact gastrointestinal tracts dissected using fine scissors. Prior to dissection, the longest dimension (diameter) of each sand dollar was measured. A 25% chlorine bleach solution (Clorox®) was added to the gut contents of each individual for 30 min to dissolve organic matter;

samples were then rinsed several times with fresh deionized (DI) water, decanted and air-dried. The gut contents of each individual were then submerged in a solution of 30% hydrochloric acid (HCl) for approximately 30 s to dissolve carbonate material. The samples were then once again subjected to several rinses with DI water, decanted and air-dried. The natural substrate sample was processed to remove organic matter and carbonate material in the same fashion as the ingested grains.

The size classes and angularity of the quartz sediment grains removed from the guts of the sand dollars ($n = 3$ adult individuals per season) and of grains from the surrounding sediment ($n = 1$ core per season) were conducted using a light microscope equipped with an ocular micrometer under $10\times$ magnification (accuracy to $10\text{ }\mu\text{m}$). A subsample of sediment from each of the 3 guts from a given season was scattered on to a glass microscope slide and immersed in mineral oil with a refractive index of 1.4920. The first 200 grains encountered under the microscope were measured for each of the 3 sand dollars. Measurements included the longest dimension of each grain and the angularity to each grain scored across 6 discrete classes (ranging from very angular to well-rounded) using the angularity scale given in Leeder (1982). This process was repeated for the first 600 grains encountered from the natural sediment sample.

Sediment ingestion experiments using live *Mellita tenuis* were conducted at the Dauphin Island Sea Laboratory (DISL), Alabama. Quartz sediments for the experiment were collected at the same location as given above in June 2007, and transported to the laboratory at Vanderbilt University. These sediments were coarsely sieved using USA standard testing sieves (Arthur H. Thomas Company) such that $>90\%$ of the size fraction that fell between 250 and $500\text{ }\mu\text{m}$ was retained (a few grains <250 and $>500\text{ }\mu\text{m}$ were retained). This size range was chosen based on the observation of Pomory et al. (1995) that *M. tenuis* prefers to consume grains within this size class. The sediment fraction was then transported to DISL in early August 2007, and incubated in artificial seawater in a flume (approximately $1.2 \times 1.2\text{ m}$ with a water height of approximately 1 m) equipped with an aquarium pump that recirculated and aerated artificial seawater. Lights were set on a 12 h light:12 h dark schedule. Following the technique of Telford et al. (1985), sediments in the flume were inoculated with a net collection of plankton for a period of 1 wk to assist in the development of a biofilm. After this 1 wk period, adult sand dollars were collected from the field site and 10 adult individuals were placed into the flume. After a 1 h period, the 3 most active (burrowing) adults (size range = 7.4 to 11.0 cm diameter) were retained and the others removed from the flume. After

72 h, each of the 3 adult individuals was turned quickly on to its aboral side, rinsed to remove surface sediments and the oral opening plugged with silicon. Sand dollars were euthanized, their guts dissected and the organic and sediment material in the guts placed into plastic, 2 cm diameter Petri dishes and air-dried. A sediment sample from the sieved sediments was also collected and processed in the same manner as sediment samples taken from the field. These samples were then transported to Vanderbilt and grain sizes and angularities measured as above.

In order to evaluate whether highly angular grains displayed surfaces analogous to those that are freshly broken (see Krinsley & Doornkamp 1973) we prepared artificially crushed quartz grains and compared them with similar-sized sediment grains from the guts of 2 sand dollars collected from the field in August and December (independent of the specimens evaluated for grain size and angularity) and from the August sediment sample using SEM. Using the quartz grain-crushing technique of Telford et al. (1985), a monolayer of quartz sand grains (from one of the natural substrate samples) was scattered across a $50 \times 75\text{ mm}$ glass microscope slide. A second similarly sized glass slide was placed on top of the slide with the sand grains and the top slide pressed down and slowly ground over the bottom glass slide for a period of approximately 1 min. Gut sediments were analyzed that had been removed from 1 adult from the summer field sample and 1 from the winter field sample. For the artificially crushed sample, the 2 sand dollar gut samples and the August sediment sample, the first 25 sand grains encountered were randomly selected using fine forceps, placed on to sputter discs, coated with platinum and photographed using SEM.

The sizes of quartz grains for each of the samples (natural substrate, sediments in flume, gut contents) were first tested for normality using the Shapiro-Wilks test for goodness-of-fit and for homogeneity of variance using an F -test (Sokal & Rohlf 1995). Because some of the data were not normally distributed, we used a chi-square analysis to compare the size-frequency distributions of grains. For the field samples (both seasons), we compared grain size frequencies of the natural substrate with size frequencies from sand dollar guts (combined from the 3 individuals) and for the laboratory samples, between sieved sediments and sand dollar guts (combined from the 3 individuals).

The angularity of quartz grains for each of the samples (natural substrate, sediments in flume, gut contents) were compared between sediment core samples from the field in both seasons or with sediments from the flume with those in the sand dollar guts by using a non-parametric G -test for independence to compare proportions of grains falling into a suite of angularity

classes (very angular, angular, subangular, subrounded, rounded and well-rounded). The G-test of independence allows an evaluation of the probability that a given grain's angularity is independent of its source (i.e. the substrate or the gut).

RESULTS

The sediments at the study site in Saint Joseph Bay in both August and December 2007 were comprised of well-sorted, medium- to fine-grained quartz-rich sand with most of the grains (>90%) occurring in the size (longest grain dimension) range of 200 to 500 μm (Fig. 1). A comparison of the size frequencies of grains in the sediments with those in sand dollar guts indicated that in both summer and winter there were significantly greater proportions of smaller size classes of grains in the guts of sand dollars when compared with those in the sediments (August, $\chi^2 = 99.1473$, $p < 0.0001$; December, $\chi^2 = 19.967$, $p = 0.0013$) (Fig. 1). These differences are primarily attributable to greater frequencies of grains that fell in the 200 to 300 μm size class.

Fig. 1. Grain size distributions of quartz grains isolated from the gut of 3 sand dollars *Mellita tenuis* (N = 600 grains) and those collected from nearby surrounding sediments (N = 600) in August and December 2007. Grain size is longest dimension as measured via light microscopy. Distributions were compared using the chi-square test statistic. Error bars are SE of the mean (N = 3)

Comparisons between grain angularities indicate that guts of 2 sand dollars in August and 1 sand dollar in December had grains in their guts that were more angular than those found in the surrounding sediments (Table 1). The remaining 3 sand dollars had guts with grains that were similar in their angularity to those in the surrounding sediments.

At the completion of the 72 h laboratory feeding experiment, the guts of sand dollars contained virtually no grains <250 μm (among the 3 sand dollars there was a mean of 1 % of total grains <250 μm). However, compared to the size classes of available grains that comprised the sieved sediments in the flume, the guts of all 3 sand dollars contained a significantly ($\chi^2 = 61.0793895$, $p < 0.0001$) higher frequency of the smaller size classes of grains that were available (i.e. 250 to 400 μm) (Fig. 2).

SEM analysis of quartz grains removed from the guts of sand dollars collected from the field in August and December and compared to quartz grains that had been crushed artificially indicated that only the artificially crushed grains displayed evidence of recent breakage, including conchoidal fractures and sharp edges (Fig. 3). In addition, grains examined from the sediment sample collected in August also did not display features of fresh breakage (images not shown).

DISCUSSION

The results of the present study indicate that guts of adults of the sand dollar *Mellita tenuis* contained a disproportionately higher frequency of the smaller size classes of quartz sand grains (200 to 300 μm) in comparison to the surrounding natural quartz sediments. The majority (75 % in August, 92 % in Decem-

Table 1. *Mellita tenuis*. Summary of results from G-test for independence testing the null hypothesis that the probability of a grain's angularity class is independent of its source. Note that only 3 out of 6 ingested grain samples were found to be more angular than the substrate samples. Significant results are in **bold**. SG: substrate grains; IG: ingested grains; values in parentheses are sand dollar diameters (cm)

Samples compared	G	p
August		
SG vs. IG (6.5)	10.665	0.0584
SG vs. IG (7.5)	50.06	<0.0001
SG vs. IG (9.2)	20.643	0.0009
December		
SG vs. IG (7.9)	20.868	0.0009
SG vs. IG (8.7)	7.445	0.1896
SG vs. IG (10.1)	3.132	0.6797

Fig. 2. Grain size distributions of quartz grains removed from guts of 3 sand dollars *Mellita tenuis* ($N = 600$ grains) after feeding for 72 h on coarsely sieved sediments ($>250 \mu\text{m}$) in the laboratory, and quartz grains taken from sieved sediments ($N = 600$). Distributions were compared using the chi-square test statistic. Error bars are SE of the mean ($N = 3$). Note that very few grains from the guts were $<250 \mu\text{m}$ (size based on measurement of the longest dimension of grains using light microscopy)

ber) of the grains found in the guts fell into larger size classes (i.e. $>200 \mu\text{m}$). In both August and December samples, less than 1% of the natural sediment was comprised of grains $<100 \mu\text{m}$ and only 2.5% of the sand grains removed from sand dollar guts were $<100 \mu\text{m}$. This pattern is similar to the observations of Ellers & Telford (1984), who studied grain size selection in the sand dollar *Echinarachnius parma* in siliceous sediments in the North Atlantic, and Telford & Mooi (1986), who studied *Encope michelini* in both siliceous and carbonate sediments in the Gulf of Mexico. Both *Echinarachnius parma* and *Encope michelini* did not select grain sizes $<100 \mu\text{m}$, but did select against larger grains. In *Leodia sexiesperforata*, which occurs solely on carbonate sediments, selection occurred for grains in the 50 to $200 \mu\text{m}$ size class (Telford & Mooi 1986). In addition, Hilber & Lawrence (in press) recently found that *Mellita tenuis* and *Encope michelini* both selected smaller particles that those found in the surrounding sediments off the central Florida gulf coast. In contrast, the sand dollar *Clypeaster subdepressus* selects only larger particles ($>200 \mu\text{m}$) in carbonate sediments (Telford et al. 1987). Not all irregular echinoids show selection for different sizes of grains: Telford et al. (1985) found that *Mellita isometra*, which inhabits siliceous sediments, ingested grain sizes at the frequency that they were available.

Fig. 3. Scanning electron microscope (SEM) images of quartz grain surfaces. (A,B) Artificially crushed quartz sand grains used as a reference for freshly broken surfaces. Arrows denote the presence of sharp edges and conchoidal fractures. (C, D) Two grains isolated from *Mellita tenuis* guts (1 from a sand dollar collected in August, 1 collected in December) that are representative of the majority of grain surfaces encountered (out of 50 grains viewed under SEM). Note that the grains do not possess sharp edges or conchoidal fractures

Differences in the ability of sand dollars to select different grain sizes may be related to the mechanics of feeding (Telford et al. 1987, Telford 1990, Pomory et al. 1995). As with many marine invertebrate deposit feeders, some species may have the ability to manipulate a particular size range of sediment grains because of differences in the morphology or mucus-secreting ability of the organs involved in food manipulation (Taghon 1982, Lopez & Levinton 1987). Physical factors that might influence the manipulability of grains of different sizes could also be important. These might include the surface texture or specific gravity of sand grains (Self & Jumars 1978). Few studies have evaluated whether sediment type (i.e. carbonate versus siliceous) has an effect on sediment size preference or feeding behavior. Hilber & Lawrence (in press) found that *Mellita tenuis* and *Encope michelini* both selected for smaller particles regardless of whether the substrate was quartz particles or carbonate shell hash.

The adaptive significance of selectivity for grain sizes among marine invertebrate sediment consumers has been framed within the constructs of the optimal foraging theory (OFT) (Taghon et al. 1978, see Pyke 1984, Cézilly & Benhamou 1996 for reviews). OFT predicts that deposit feeders will select greater proportions of the smaller size classes of sediments so as to optimize the consumption of organic material that coats sand grains (Taghon et al. 1978, Taghon 1982). As grain size decreases, the amount of available food coating the grain surface exponentially increases (Taghon et al. 1978, Hammond 1982). A variety of groups of marine invertebrate deposit feeders have demonstrated preferences for smaller grains including polychaetes (Hylleberg 1975, Pardo & Dauer 2003), bivalves (Hylleberg & Gallucci 1975, Ward & Shumway 2004), echiurans (Jaccarini & Schembri 1977) and thalassinidean shrimp (Stamhuis et al. 1998). The present study lends further support to the OFT in that *Mellita tenuis* selected smaller grain sizes.

The present study did not directly investigate whether *Mellita tenuis* selects smaller sizes of grains using the specialized tube feet located on the oral surface. Nonetheless, we employed a 3-pronged indirect approach to test the hypothesis that the smaller grains we observed in the guts of *M. tenuis* were the result of selection rather than grain crushing by the Aristotle's lantern. First, we compared the degree of angularity of grains removed from the guts of sand dollars to those of the surrounding sediments. Our prediction that, if individuals were crushing the grains, then guts should consistently harbor grains with a greater degree of angularity, was not supported by our observations (50 % of the 6 individuals examined did not have more angular grains in their guts). However, because some individuals had more angular grains in their guts, we

cannot rule out the possibility that crushing could be occurring occasionally. Second, we used SEM to determine if the surfaces of grains removed from the guts of individuals from the field had sharp edges and conchoidal fractures representative of recent breakage. We found that the grains removed from guts did not resemble grains that had been artificially broken; that is, in large part they lacked sharp edges and conchoidal fractures. Finally, under controlled laboratory conditions, we found that *M. tenuis*, when presented quartz sediments within the natural range of sizes ingested, yet manipulated such that the smaller size classes were removed (<250 µm), did not yield guts with smaller size classes of grains (i.e. <250 µm). If, in fact, individuals used their teeth to crush the quartz sand grains, then our expectation was that there would be many small grains present in the guts following feeding.

In a study with a closely related species, Telford et al. (1985) found that despite only 10 % of the natural sediments being comprised of grains <100 µm, over 90 % of the sand grains removed from the guts of *Mellita isometra* fell into this small size class. They attributed the abundance of small quartz grains in the guts to the crushing activity of the teeth during ingestion. In the present study on *M. tenuis* there was little evidence of grain crushing. This result is supported by Hilber & Lawrence (in press), who suggested that the presence of smaller particles in the food grooves of *M. tenuis* made grain crushing unnecessary, which explained the presence of smaller particles in the gut. Inter-specific comparisons of the teeth of echinoids indicate they possess similar material hardness (Klinger & Lawrence 1985). Due to the differences in tensile strength, it is unlikely that echinoids, which have high-magnesium calcite teeth (Markel 1977, Ma 2007), are capable of crushing much higher tensile strength quartz sand grains. As an alternative explanation for the presence of smaller grains within the gut, particle selectivity may also occur post-ingestion as grains are processed through the gut. It has been shown that the morphological adaptations (e.g. gut pouches) of the digestive tracts of both deposit and suspension feeders may function to increase the gut residence time of preferred particles (Self & Jumars 1978, Bricelj et al. 1984, Brillant & MacDonald 2000, Ward & Shumway 2004). For example, it has been shown that preferred particles (based on either physical or chemical characteristics such as size and the presence of organic coating) are retained within the gut of the sea scallop *Placopecten magellanicus* for longer periods of time, whereas other particles are evacuated more quickly (Brillant & MacDonald 2000, 2002, 2003). This may allow further digestion and/or detachment of organic material from particles. In the future, analysis of grain

size distributions from the surrounding sediment, the gut and the feces may serve to confirm whether grain selection occurs within the gut in *M. tenuis* and other representatives of the genus.

The sedimentological and ecological implications of sediment sorting by marine invertebrate deposit feeders are significant (Rhoads 1974, D'Andrea et al. 2004, Kogure & Wada 2005). Like irregular echinoids in general, most sand dollars ingest large amounts of sediments (Lawrence & Sammarco 1982). Moreover, they often occur in remarkably high densities (e.g. 820 ind. m⁻²; Salsman & Tolbert 1965) in nearshore sediments around the world. While often considered relatively immobile, this can be a misconception as some species may move through sediments at 1 to 15 cm h⁻¹ (Findlay & White 1983) and may disrupt up to 14 % of the upper sediment surface per hour (Reidenauer 1989). Despite the potential that sand dollars have to impact nearshore environments, this topic has received relatively little attention. The main physical impacts of sand dollars on sediments include size-sorting of sediment grains (Bell & Frey 1969), extensive reworking of surficial sediments (Salsman & Tolbert 1965, Stanley & James 1971, Sisson et al. 2002) and an increase in the zone of oxidized sediments (Findlay & White 1983). Biologic impacts include significant alterations to infaunal community structure including population impacts on foraminifera (Findlay & White 1983), harpacticoid copepods (Creed & Coull 1984, Reidenauer 1989) and nematodes (Creed & Coull 1984), as well as the microbial community (Findlay & White 1983). The present study indicates that *Mellita tenuis* impacts the community by sorting sediments. However, at least in *M. tenuis*, it appears unlikely that individuals crushed grains, and thus do not directly contribute to sediment alteration through this process.

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