ABSTRACT: Pycnodonte newberryi oysters accumulated in voluminous shell beds of Late Cretaceous (late Cenomanian) age in shale deposits of the Western Interior Seaway. Analysis of triplicate grid samples from six shell beds in southern Utah shows that the reclining valves of the oyster are disproportionately represented by the inflated left valve, eight times more often than the smaller, flat right valve, and whole valves are rare. The shells nearly always fragment from the commissure toward the thick umbonal half of the shell. These fragmented shells make up more than half of grid samples, and only 0.5% contain predatory drillholes. By contrast, complete shells are drilled nearly 5% of the time, particularly near the umbo. Fragmentation cannot account for this discrepancy because the preponderance of drillholes occurs in the umbonal part of the shell, the part that is always preserved. To understand this paradox, drilled Pycnodonte were collected from a separate site in Utah and drillhole position on the shell was mapped to create a probabilistic model of drillhole sites. Results show that > 60% of drillholes are positioned in the robust part of the umbonal shell, confirming observations in the unfragmented grid-sampled shells. We propose that the deficit in drilled shell fragments can be explained by spatial or temporal mixing of two populations of Pycnodonte that lived under separate predation pressures. Autochthonous shells show greater drillhole incidence and shell completeness, whereas fragmented umbonal shells indicate transportation from a separate environment having lower predation pressure. This study indicates that taphonomic mixing may introduce significant bias in drilling incidence.

INTRODUCTION

The formation of oyster shell beds and what they might indicate about past predation pressure is the subject of this study. Large shell accumulations involve a broad range of taphonomic processes, including disarticulation, fragmentation, transportation, and bioerosion, each process degrading the original specimen and potentially obscuring the primary ecological signal of predation (e.g., Lever et al. 1961). Kowalewski (2002) reviewed the role of taphonomy on predatory evidence in shells, and offered sampling protocols to recognize or minimize potential biases. Here we present an example of widespread shell accumulations that seem to indicate a strong taphonomic bias, where increased degree of fragmentation corresponds with a decreased incidence of predatory drillholes. Taphonomic analysis suggests, paradoxically, that the process of fragmentation is not the explanatory mechanism in the study material.

Oyster shell beds are common within the Late Cretaceous Western Interior Seaway of North America, and contribute significantly to the benthic biomass (Kirkland 1990, 1996; Harries and Schopf 2003; Congreve et al. 2005). During the latest Cenomanian, Pycnodonte bivalve shells were especially abundant, forming laterally continuous, nearly monospecific coquinas in the Four Corner States, including southern Utah (Stanton 1893; Hook and Cobban 1977; Kirkland 1996). These shells are gryphaeid in form and are referred colloquially as Devil’s Toenails. They have a deeply convex, thick left valve and a small planar right valve. A scar on the left valve demonstrates an early attached habit,
but as adults their broad flange-like commissure allowed them to recline on the soft muddy seafloor (Hallam 1968; Stanley 1970; Stenzel 1971). The reclining lifestyle of benthic fauna shows a steep decline by the end of the Mesozoic Era, possibly in response to increased marine bioturbation (Thayer 1979; LaBarbera 1981).

Gryphaeid oysters were also under increasing predation pressure during the Late Cretaceous. For example, along the Atlantic coast, Dietl et al. (2000) demonstrated morphological changes in Campanian–Maastrichtian gryphaeids in response to shell-crushing predators. Predation by shell-drilling gastropods was on the rise during the Late Cretaceous (Taylor et al. 1980; Vermeij 1987; Kelley and Hansen 1993; Harries and Schopf 2007). Yet, drilling predation in the Western Interior Seaway appears to lag by comparison to contemporaneous deposits along the Atlantic Coastal Plain. The results presented here on pre-Campanian drillholes add new information to the Western Interior record of Mesozoic predation.

GEOLOGIC SETTING

The Late Cretaceous Western Interior Seaway flooded the Sevier Foreland Basin and bisected North America. The westernmost transgression of the seaway is marked by the Cenomanian deposition of the Tropic Shale over coastal sandstone of the Dakota Formation. The lower part of the Tropic Shale preserves abundant *Pycnodonte* bivalves. Three main sites, Bigwater (BW), Lefthand Collet (LHC), and Highway 12 (HWY12) were chosen for this study within the Kaiparowits Basin (sites 1 to 3 on Fig. 1, respectively). Here, the contact between the Dakota Formation and the Tropic Shale is well exposed and the presence of prominent bentonite and limestone marker beds in the Tropic Shale (*sensu* Elder 1991) permit excellent correlation between sampling localities. The *Pycnodonte* shell beds investigated in this study lie within the basal 12 m of the Tropic Shale, which is characterized by fine-grained bentonitic mudstone of shallow, normal-marine origin and a suite of interbedded, bentonitic claystone interpreted as primary airfall ashbeds (Fig. 2, Gregory and Moore 1931; Cobban et al. 2000; Titus 2004; Titus et al. 2005). Most of the sampling sites are constrained to rocks between the Dakota-Tropic contact and the ~93.9 Ma “B” bentonite horizon of late Cenomanian age (Elder 1991; Obradovich 1993; Titus et al. 2005). The *Pycnodonte* shell beds investigated in this study co-occur with rare ammonites, gastropods, and other oysters, and many of these richly fossiliferous horizons are associated with concretionary carbonate horizons in the bentonitic mudstone facies. An additional site (4 on Fig. 1) was selected in the Henry Basin located 80 km to the northeast near the town of Hanksville, Utah (Stop 1 on HWY 24 in Fielding et al. 2010). The transgressive unit overlying the Dakota Sandstone here is called the Tununk Shale Member of the Mancos Shale, and it is genetically equivalent to the Dakota-Tropic contact in the Kaiparowits Basin to the southwest. The base of the Tununk Shale records a *Pycnodonte* shellbed in a mudstone matrix that forms the top of bluffs for hundreds of meters.

MATERIALS AND METHODS

Grid sampling of *Pycnodonte* shells was conducted at the three localities in southern Utah for a total of six sampling localities. At each locality, the shell beds were sampled in triplicate from surface exposures in 1m² grids spaced within 20 m along bedding planes. Triplicate sampling was chosen to monitor variance in individual grid samples, especially considering the low frequency of drillholes. Shells were cleaned and sieved to retain fossils > 8 mm. This minimum size decision was made to avoid underestimating drillhole frequency (Kowalewski 2002) and also served a pragmatic function of limiting shell counts to include specimens that might record drillholes up to 4 mm in diameter. We examined several of the < 8 mm sieve fractions and found no examples of drillholes, including those located at the margin of a fragment. Taphonomic characters were noted for all grid samples, including articulation, fragmentation (edge rounding, fracturing, and spalling), bioerosion, and encrustation. Only fragments recording 50% or more of the original shell were analyzed in this study. The fragments are categorized into four fragment classes, consisting of 50%, 75%, 90%, and 100% complete (Fig. 3). These fragments always retained the umbo.
Circular drillholes referable to *Sedilichnus* (previously, *Oichnus*; see Zonneveld and Gingras 2014) were measured and described in the context of the target shell. Complete and incomplete drillholes were mapped according to their position on the shell using a six-sector map of the left valve. Morphometry of drillholes was quantified using digital calipers. Depth of borings was occasionally obscured by cemented matrix fill.

Given the rarity of drilled *Pycnodonte* at other localities, a separate *Pycnodonte* shellbed locality at Hanksville was selected to make a collection of complete *Pycnodonte* shells, especially ones with *Sedilichnus*. This provided a large dataset of *Sedilichnus*-bored shells with which to compare sector distributions and morphology of the borings. Borings were mapped following the six-sector map used for the grid samples. In addition, several Hanksville *Sedilichnus* were cast using Epofix under low vacuum and the shell etched with dilute HCl (Nielson and Maiboe 2000). Cast specimens were coated with carbon and imaged under SEM with an electron beam density of 30.0 kV. Specimens are repositored at the Idaho Museum of Natural History, Pocatello.

**RESULTS**

**Occurrence and Physical Taphonomy**

Triplicate grid sampling generated 4,822 *Pycnodonte* specimens from the six sampling horizons at the three localities (Table 1). Overall the inflated, convex left valves dominate the collections (89.0%) by comparison to the flat right valves (10%), and articulated paired valves are rare (0.64%). Individual localities show a broader, but self-consistent range of LV:RV (left valve : right valve) ratios, where left valves represent 80%–100% of the assemblage. The Big Water locality (unit 1) is the only exception, where right valves comprise up to 70% of the grid sample. Because of the dominance of left valves in these assemblages, observations presented below refer exclusively to the left valves, unless otherwise stated.

Shell fragmentation is ubiquitous, affecting 98.5% of shells in this study. Roughly half of the specimens are ~ 50% complete. As specimens having less than 50% shell are excluded from these counts, fragmentation is even more common than the value calculated. Owing to the relative thickness and convexity of the umbonal region, the dorsal half of the left valve is most commonly retained. The fragmentation process consumes shell from the commissure toward the umbo. The posterior shelf is commonly absent in all but the most complete specimens. Edge chipping and delamination (spalling) of the shell are the most commonly observed modes of fragmentation. There is no evidence for shell repair from premortal shell chipping, tearing, or crushing.

The defined fragmentation classes show diminishing contribution with increased level of completeness to the total number of specimens in the grid samples (Fig. 4). Although a rare component of most of the studied assemblages, right valves tend to be well preserved and intact.

**Entobia and Caulostrepsis Borings**

Borings in the shells include common *Entobia* and rare *Caulostrepsis*, and these are found in 14% and 0.4%, respectively, of *Pycnodonte* shells in this study (Table 1, Fig. 3). *Entobia* cavities are interconnected networks of spherical chambers and narrow canals that sometimes form distinct pinprick apertures at the shell surface (Fig. 3B, C). These cavities are most likely produced by clionid sponges (Bromley 1970), and are observed in both internal and external surfaces of the *Pycnodonte* shells. *Caulostrepsis* (Fig. 3D) is a U-shaped boring roughly parallel to the shell surface often ascribed to the activity of polydorid worms (Bromley and D’Allesandro 1983). Both *Entobia* and *Caulostrepsis* are common Cretaceous marine borings that represent postmortem domichnia (Bromley 2004).

**Sedilichnus Borings**

*Sedilichnus* drillholes occur in 37 of the 4,822 *Pycnodonte* specimens (< 1%), one-third are incomplete. *Sedilichnus* borings (Fig. 5, Supplementary Data Table 1) are circular in outline, and penetrate perpendicular to the outer shell surface and have straight, subparallel margins. Most incomplete borings have a smooth, concave bottom; however, at least three specimens show evidence
for a marginal boss (described below). The upper edge of the *Sedilichnus* borings is slightly wider at the aperture than the base, and is not beveled.

*Sedilichnus* range in diameter from 0.62–4.5 mm. Complete drillholes extend down through as much as 6.5 mm of *Pycnodonte* shell; a very slight taper can be observed in the deepest of penetrative borings.

Epoxy casts of several *Sedilichnus* show xenoglyphic patterns owing to the laminar-vesicular (Kirkland 1996) shell ultrastructure. Bioglyphs, such as parallel grooves made from radular scraping (Schiffbauer et al. 2008), are absent in all but one specimen. In this incomplete drillhole, the base and margin of the boring has a boss, or incompletely excavated portion, that projects upward from the bottom of the concave drillhole. The boss has four curved, concentric terraces (0.6, 0.3, 0.3, and 0.8 mm wide) that stair-step upward to the margin of the boring’s base (Fig. 5F, G). Subparallel scratches with a spacing of 53–57 µm ornament the terraces. Two other incomplete borings from Hanksville record marginal bosses, although they are not terraced nor do they show scratch traces.

**Drilling Distribution**

Although affecting <1% of the total *Pycnodonte* specimens, the occurrence of *Sedilichnus* ranges by locality from a high of 4.2% at LHC (unit + 3.75 m, grid 1) to 0% in the HWY12 and BW U1 localities. Of the drillholes in grid samples, two-thirds are complete, and two shells have evidence of incomplete and complete (i.e., multiple) drillholes. Sector mapping shows that the majority of *Sedilichnus* are in the umbonal region encompassing dorsal sectors 1 and 2 (Fig. 6A–E, Supplementary Data Table 2). The shell is thickest in these sectors, up to ~ 7 mm in the largest *Pycnodonte*. The pattern of fragmentation in this taxon favors the preservation of the umbonal portion of the shell, which might bias the observation of *Sedilichnus* drillholes. Figure 4 shows that, although more than half of sampled *Pycnodonte* are in the 50% fragment class, this class only accounts for 13% of all drillholes in the sample. Compared to all drilled shells in the grid sample, more than two-thirds of *Sedilichnus* occur in the umbonal sector.

**The Paradox of Fragmentation and *Sedilichnus***

To understand the relationship of fragmentation and *Sedilichnus* placement, we surface collected at the Hanksville locality 196 complete *Pycnodonte* left valves, 88 of which record *Sedilichnus*. During collection, two right valves were found to contain *Sedilichnus* borings and represent the only bored right valve specimens in our study.

The Hanksville collection of left valves contained 50 complete and 41 incomplete *Sedilichnus*, and four of the shells contained multiple drillholes, numbering no more than three in a single shell. The morphology of the drillholes matches those found at LHC, HWY12, and BW. The sector map (Fig. 6C) shows 60% of the drillholes are in the umbonal sectors 1 and 2, roughly corresponding to the part of shell preserved in the 50% fragmentation class. The general sector pattern of *Sedilichnus* in complete shells from Hanksville strongly resembles the pattern of *Sedilichnus* from the grid-sampled localities (Fig. 6B; $\chi^2 = 10.9$, significant at $\alpha = 0.05$).

The sector map data from Hanksville are used to model the expected frequency in the grid samples from LHC, HWY12, and BW (Fig. 7). The drillhole morphology and distribution on the shells (Fig. 6B, C) are very similar among all localities, lending confidence to the extrapolation of Hanksville samples to the other localities. Assuming the distribution of *Sedilichnus* in complete shells at Hanksville is roughly equivalent to the distribution of *Sedilichnus* in complete shells in the grid samples (Fig. 6B, C), we use the actual number of fragments from the grid samples to calculate an expected value for *Sedilichnus* in each fragment class (Table 2). For grid-sampled specimens (LHC, HWY12, BW) that are 90% to 100% complete, the actual values plot at a 5% drilling frequency, but as fragmentation is more severe, the actual values decline to boring frequencies below 2% and 1% for the 75%–50% fragment classes. In other words, if drilling frequency affected 5% of the *Pycnodonte* population, the 75% and 50% fragment classes are underrepresenting this signal by 4×–13×, respectively. The observed decline in boring frequency for smaller fragments is counterintuitive because the great majority of drillholes in our
complete specimens (Hanksville and all grid-sampled specimens; Fig. 6) are found in the umbonal part of the shell, which is not subject to fragmentation observed in this study.

DISCUSSION

Mixed Assemblage Mechanism for Drilling Bias

*Pycnodonte* shell beds are renowned for their lateral continuity and nearly monospecific assemblages throughout the mid-Cretaceous midshelf deposits of southern Utah. Biostratinomy and fragmentation documented in this study suggest transport and concentrating processes resulted in the shell beds. Whole specimens are rare, and more significantly, the inequivalve shells are deposited separately from one another. Although shell beds usually feature 80% to 90% left valves, we have found at least one locality where right valves are concentrated in greater abundance. The comparative rarity of *Pycnodonte* right valves is striking; although this study collected 500, only two contained *Sedilichnus*. Nonpredatory borings by sponges and worms commonly affect one fifth or more of the shells, suggesting prolonged exposure of the shells to oxygenated, clear water prior to ultimate burial (Davies et al. 1989).

Evidence of *Sedilichnus* drillholes is not evenly distributed across fragmentation classes. Greatly fragmented shells (e.g., 50% fragment class) show lower drillhole frequency than do more complete shells. This result could be explained as a decreased probability of finding a drillhole when less original shell is preserved, or that fragmented shells having drillholes might be transported differently than those without drillholes (e.g., Lever et al. 1961). But this is not the case in *Pycnodonte* shell beds. Sector maps derived from both grid sampling and selective whole-shell sampling demonstrate that a great majority of drillholes are recorded in the umbonal part of the shell (sectors 1 and 2), and this region is always preserved in the studied specimens. Resolving this paradox requires an alternative mechanism to explain why umbonal shell fragments record a disproportionately small number of umbonal drillholes.

We posit that most shellbeds are made up of a mixed assemblage of autochthonous and parautochthonous shells (Fig. 8). The autochthonous group includes mostly complete individuals (90%+ fragment class) and boring frequencies of ~ 5%, whereas transportation of the parautochthonous shells results in greater fragmentation (50%–75% class). Parautochthonous shells record a separate environment having a lower predation pressure and boring frequencies below 1.5%. This scenario accounts for the taphonomic bias in drilling frequency not caused by fragmentation (i.e., deleting the predation record), but rather by mixing two shell populations having different ecological histories. This is exemplified by the localities from LHC and BW unit 10, which are dominated (> 80%) by highly fragmentary shells and have ~ 1% *Sedilichnus* frequency. The infrequently bored shell fragments dilute the autochthonous, more complete, and more frequently drilled shells.

In shell beds that show lesser degrees of reworking and transport, such as localities BW unit 1 and HWY12, we record no evidence of *Sedilichnus* predation. Instead, both localities have poor sorting of left and right valves and a higher proportion of complete shells. These may represent an unmixed census-style assemblage from the low-predation environment similar to the parautochthonous cohort (fragmented, undrilled shells) found in the mixed assemblages.

The model for *Pycnodonte* shellbed formation could be accommodated by some combination of spatial or temporal mixing. In the spatial example (Fig. 8A), shells having low boring frequency (< 1.5%) are transported, fragmented, and deposited among autochthonous shells having a high boring frequency (5%). The ecological inference is that contemporaneous *Pycnodonte* populations had different predation pressure owing to position along the shallow marine shelf. By contrast, the temporal explanation (Fig. 8B) is that shells of low boring frequency from an earlier time were reworked, fragmented, and redeposited in the same environment that had increased in predation pressure, as recorded by the more complete shells in the assemblage.

Because greater fragmentation accompanies lower boring frequency, the mixture of shells is asymmetric in the sense that the fragmented, 1.5%-bored shells are always mixed with the complete 5%-bored shells, and not the reverse. From a temporal mixing point of view, this requires that the
earlier shell assemblage always has lower predation pressure than the autochthonous shell group. While predation pressure might vary over time, there is no a priori expectation that it should always increase in magnitude until ultimate deposition. Instead, spatial mixing is more likely to generate the asymmetric pattern observed here. One possibility is that the parautochthonous shells may have originated nearer to shore with either brackish or hypersaline waters that mitigated stenohaline predators, and these were subsequently mixed with a seaward (autochthonous) population where more normal salinity accompanied greater predation pressures (Fig. 8A).

Cretaceous Sedilichnus

The incomplete drillhole is unique in the Cretaceous collections, but strongly resembles the crescent-and-boss morphology made by the proboscis of modern Polinices and Murex borers (Carriker and Yochelson 1968, pl. 2, figs. 8, 20, 21). Terraces suggest a series of curved excavations, starting at one side of the boring and proceeding to the opposite; a pattern that if interrupted could produce a crescent-and-boss morphology. With the additional evidence of microscopic parallel scratch traces on the terraces, the Cretaceous Sedilichnus borings are most likely the product of gastropod predation. Determining a more specific predatory clade is not possible at this time. The gastropods Euspira and Eunaticina (contentiously assigned to the Naticidae; Aronowsky and Leighton 2003; contra Kase and Ishikawa 2003) and the eulimid, Eulima, are reported to co-occur with Pycnodonte newberryi at the Big Water locality (Elder 1987), although none were found in this study. No muricid gastropods are known from the Western Interior during this time interval.

While the Late Cretaceous of the Atlantic Coastal Plain has received the most detailed research in drilling and shell-breakage predation (e.g., Kelley and Hansen 1993; Dietl et al. 2000), recent efforts on the Western Interior Seaway in the United States has produced interesting comparative results. A survey approach by Schof (1993) found little to no occurrences of drilling predation in the Cretaceous of the Western Interior, but later reports on inoceramid predation (Harries and Ozanne 1998; Ozanne and Harries 2002; Harries and Schof 2003) and broader study of Maastrichtian mollusks demonstrate at least 3% boring frequency in the WIS (Harries and Schof 2007). These values are significantly lower than Late Cretaceous predation frequencies of 13%–19% in the Coastal Plain (Kelley and Hansen 1993), and support the notion that the greater longevity of the Atlantic Basin as compared to the Western Interior Basin resulted in the evolution of enhanced predation pressures (Harries and Schof 2007).

CONCLUSIONS

Pycnodonte shell beds in southern Utah are an amalgam of transported and in situ populations. Fragmentation of shells corresponds with lower occurrence of Sedilichnus predatory drillholes, which most likely reflects a reduced predation pressure in the onshore environment from which the shells were transported. The in situ population of shells in the depositional environment displays up to 5% Sedilichnus frequency. In this instance, taphonomic mixing of shell populations, not fragmentation, diluted the signal of predation pressure in the depositional environment. Scratch traces associated with peripheral terraces on incomplete drillholes suggest these are the product of gastropods, although tracemaker fossils are absent in the shellbed deposits.

ACKNOWLEDGMENTS

Fieldwork and funding for the project were supported by the Bureau of Land Management (BLM), Grand Staircase–Escalante National Monument (grant JSA 055008). We thank D. Powell, A. Titus, and S. Foss (BLM) for providing significant logistical support with permits and fieldwork. Fossil specimens were collected under BLM permit UT06-007S.

SUPPLEMENTAL MATERIAL

REFERENCES


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Received 6 July 2014; accepted 3 February 2015.

FIGURE CAPTIONS

FIG. 1.—Field localities in southern Utah include (1) Big Water, (2) Lefthand Collet, (3) Highway 12, and (4) Hanksville.

FIG. 2.—Stratigraphy of Cretaceous field localities. Hanksville section based on Fielding et al. (2010).

FIG. 3.—Taphonomy of *Pycnodonte* shells. A) Fragment classes from 100% complete to 50% complete; the umbal region is most robust part of shell. B, C) *Entobia* sponge borings in apertural and cross-section views. D) *Caulostrepsis* on external shell.

FIG. 4.—Proportion of grid-sampled shells in each fragment class. Shells bored with *Sedilichnus* are disproportionately complete by comparison to all shells in the sample.


FIG. 6.—Distribution of *Sedilichnus* in *Pycnodonte* shells. A) Sector map and fragment classes are generally aligned. B, C) Sector maps of *Sedilichnus* in grid samples and in selective (Hanksville) sample show similar distributions. D, E) Boring frequency in grid samples and Hanksville sample are the greatest in the the umbal sectors 1 and 2, including incomplete borings.

FIG. 7.—Actual versus expected incidence of *Sedilichnus* drillholes for the four fragment classes. Actual values based on grid samples at LHC, HWY12, and BW localities; expected values based on distribution observed at Hanksville.

FIG. 8.—Taphonomic model of spatial and temporal mixing that could result in the *Pycnodonte* shell beds. A) Spatial mixing. B) Temporal mixing. Shells from an environment of low predation pressure (yellow) are transported (or reworked) and mixed with the autochthonous, high predation-pressure shell population (red). Greater fragmentation correlates with reduced predation pressure and lower *Sedilichnus* frequency.

TABLE CAPTIONS

TABLE 1.—Taphonomic data for grid shell sampling (Grids 1 to 3) for Lefthand Collet, HWY12, and Big Water localities. Count data followed by percentages in parentheses. *Caul* = *Caulostrepsis*, LV = left valve, RV = right valve.

TABLE 2.—Position of *Sedilichnus* drillholes in Hanksville sample used to calculate expected values for comparison to actual grid samples at LHC, HWY12, and BW.
<table>
<thead>
<tr>
<th>Locality</th>
<th>N</th>
<th>Complete</th>
<th>Incomplete</th>
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<tr>
<td>LHC 0.7</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LHC 3.0</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LHC 3.75</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BigWater</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Hanksville</td>
<td>91</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

A. Fragment Class

B. Grid Samples

C. Hanksville

D. % location of all drillholes

E. % location of all drillholes
Drilling frequency gradient

Fragment class:
- 50-75%
- 90-100%

Drilling frequency gradient:
- 0.5%
- 5%

A
- Time 1: Depocenter
- Time 2: Storm reworking & transport
- Autochthonous

B
- Time 1: Depocenter
- Time 2: Local reworking
- Time-averaged autochthonous

parautochthonous + autochthonous
<table>
<thead>
<tr>
<th>Locality</th>
<th>N</th>
<th>Entobia</th>
<th>Caul</th>
<th>Sedilichnus</th>
<th>LV</th>
<th>RV</th>
<th>Whole</th>
<th>50%</th>
<th>75%</th>
<th>90%</th>
<th>100%</th>
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<tr>
<td>LHC +0.7m G1</td>
<td>462</td>
<td>39 (8.4)</td>
<td>2 (0.4)</td>
<td>4 (0.9)</td>
<td>411 (89.0)</td>
<td>47 (10.2)</td>
<td>4 (0.9)</td>
<td>186</td>
<td>204</td>
<td>67</td>
<td>5</td>
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<tr>
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<td>13 (17.1)</td>
<td>0</td>
<td>0</td>
<td>76 (100.0)</td>
<td>0</td>
<td>0</td>
<td>35</td>
<td>37</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>LHC +0.7m G3</td>
<td>66</td>
<td>30 (45.5)</td>
<td>3 (4.5)</td>
<td>0</td>
<td>54 (81.8)</td>
<td>6 (9.1)</td>
<td>6 (9.1)</td>
<td>30</td>
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<td>279</td>
<td>66 (23.7)</td>
<td>0</td>
<td>1 (0.4)</td>
<td>249 (89.2)</td>
<td>30 (10.8)</td>
<td>0</td>
<td>153</td>
<td>90</td>
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<td>330 (89.2)</td>
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<td>5 (4.2)</td>
<td>114 (95.8)</td>
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<td>50</td>
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<td>51 (34.0)</td>
<td>1 (0.7)</td>
<td>1 (0.7)</td>
<td>145 (96.7)</td>
<td>3 (2.0)</td>
<td>2 (1.3)</td>
<td>95</td>
<td>40</td>
<td>12</td>
<td>3</td>
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