

# Drilling predation on Permian brachiopods and bivalves from the Glass Mountains, west Texas

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Although bored invertebrates have been described from every period of the Paleozoic, little information on the frequency and nature of Late Paleozoic drill holes exists. Our examination of the Permian silicified fossils, which were bulk collected by G.A. Cooper from the Glass Mountains of west Texas, revealed numerous drilled brachiopods and bivalve mollusks. Drill holes are perpendicular to the shell, smooth sided, sometimes beveled, and have other characteristics consistent with a predatory/parasitic origin. The frequency of drilling is significantly lower ( $p \leq 0.05$ ) for brachiopods (1.07%,  $n = 7597$ ) than for bivalves (7.43%,  $n = 619$ ). This study confirms that drilling predators and/or parasites were present in the Late Paleozoic. However, the drilling frequencies reported here—rarely exceeding 5%—are much lower than those reported for the Late Mesozoic and Cenozoic, which typically exceed 20%. The low Late Paleozoic frequencies are consistent with a majority of estimates reported previously for the older periods of the Paleozoic and suggest that the intensity of drilling predation/parasitism in marine benthic ecosystems remained low throughout the Paleozoic and did not increase until some time in the Mesozoic. Our data suggest that prey/host types with a higher nutritional return (bivalve mollusks) may have been preferentially selected for attack by predator(s)/parasites(s) already in the Permian.

**Key words:** Drilling predation, drilling parasitism, Paleozoic, brachiopods, bivalve mollusks, Texas.

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## Introduction

The opportunity to study individual interactions in the fossil record and the chance to document a predator-prey system in an evolutionary context has led to considerable interest in drilling predation. In particular, the hypothesis of escalation proposed by Vermeij (1987) can be tested rigorously using drilled prey fossils both from the ecologic evolutionary perspective (e.g., Kelley and Hansen 1996) as well as from the point of view of functional morphology (e.g., Dietl et al. 2000; Leighton 2001). However, most of the large-scale quantitative studies to date have focused on the Cenozoic, a time interval during which drilling predation has been a common phenomenon (e.g., for recent reviews and numerous references see Kowalewski and Kelley 2002; Kelley et al. 2003). In contrast, the record of drill holes is more controversial for the Paleozoic (see Brett and Walker 2002; Baumiller and Gahn 2002; Brett 2003; Leighton 2003 and numerous references therein). Whereas many of these drill holes may have been non-predatory in nature (e.g., substrate borings;

Richards and Shabica 1969), it appears that at least some of the drillings observed in Paleozoic brachiopods are predatory or parasitic in origin (e.g., Sheehan and Lesperance 1978; Ausich and Gurrola 1979; Kowalewski et al. 2000; Leighton 2001; Hoffmeister et al. 2003).

This study reports extensive quantitative data on drilling in Permian bivalves and brachiopods from West Texas assembled using the extensive Cooper collections housed in the Smithsonian Institution National Museum of Natural History. The Permian brachiopods and bivalves are a particularly worthy target because the Late Paleozoic record of drilling behavior has received very limited attention so far and because there are very few reports of drilling predation in Paleozoic bivalves (e.g., Kowalewski et al. 2000).

Based on a literature survey, Kowalewski et al. (1998) proposed three distinct intervals in the history of drilling predation. They suggested that this behavioral strategy was present throughout much of the Paleozoic, but noted that frequencies of drilling were much lower than those reported for the Late Mesozoic and Cenozoic. Of particular interest is the “Meso-

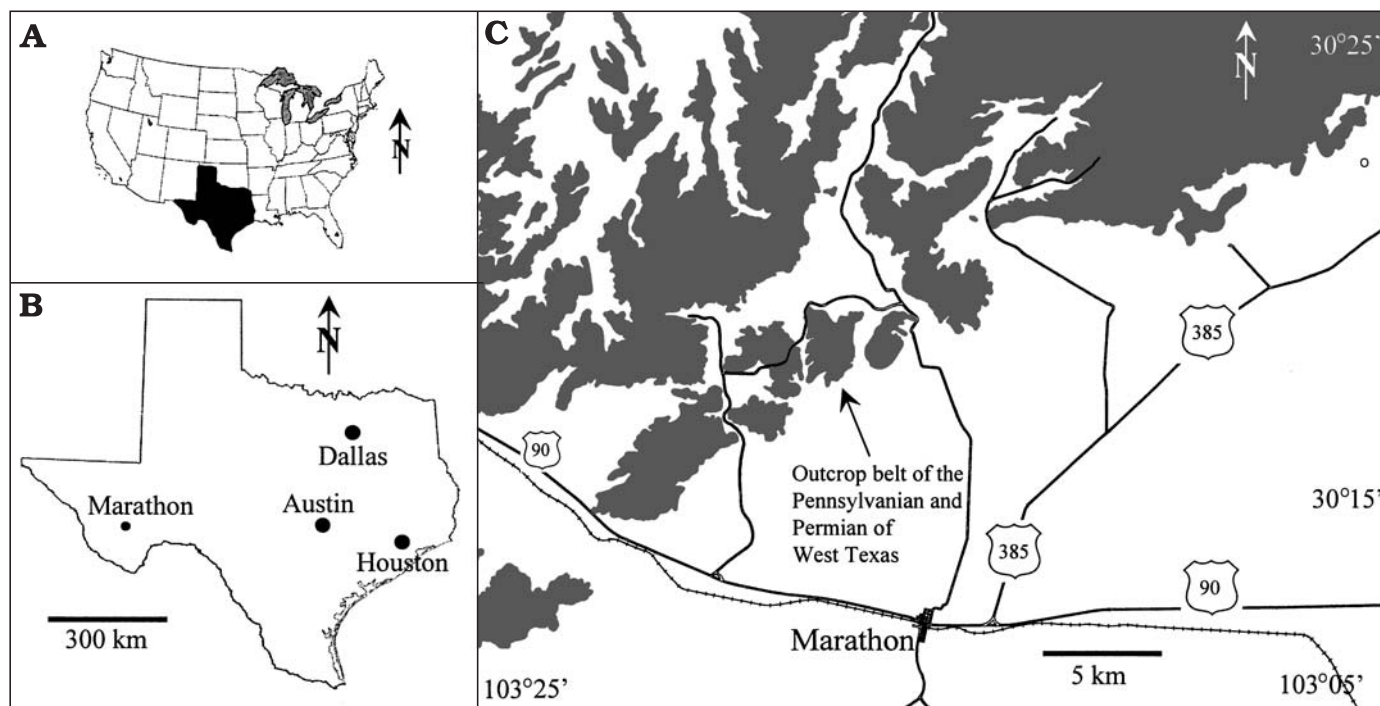


Fig. 1. Study area. **A.** Location of Texas within the United States. **B.** Location of the city of Marathon with respect to other cities in Texas. **C.** Location of the Glass Mountains in the area of Marathon, Texas (modified from Cooper and Grant 1972).

zoic Phase” (Permian–Early Cretaceous) characterized by very low drilling frequencies interpreted by Kowalewski et al. (1998) as a time interval when the predators were facultative and only drilled rarely. However, this interval has very few reported data points and this study aims to provide new insights into this under-researched time interval.

In addition, this project allows us to compare drilling predation between two morphologically and ecologically similar groups that differ notably in various aspects of their biology and have had very disparate evolutionary histories. The desirability of such a comparison has long been recognized (e.g., Thayer 1981), yet we know of no direct comparison of drilling intensities between contemporaneous bivalves and brachiopods in the literature to date. This type of analysis is especially important in understanding the Paleozoic drilling predator-prey systems. The differences in tissue mass (typically higher for bivalves), shell thickness (brachiopod shells tend to be thinner), shell composition and structure (calcitic for most brachiopods and often aragonitic or mixed for bivalves), prey habitat (brachiopods are generally epifaunal whereas at least some Paleozoic bivalves were infaunal), and relative abundance in fossil assemblages (brachiopods tend to dominate many fossil assemblages in the Paleozoic; but see Cherns and Wright 2000), all may provide insights into the nature of driller-prey/host interactions.

Most previous studies of Paleozoic drilling behavior have dealt with collections from a single locality, which represent short time frames (but see Alexander 1986 and Leighton 2001 for studies that do address predation through time). These studies are important because they show that drilling

behavior existed at some period in time, but of equal importance is to understand how drilling patterns changed through time. This study examines strata from Texas that span much of the Permian, thus allowing for investigation of temporal trends within that time frame.

The extensive quantitative dataset of Permian drill holes assembled here allows us to compare these new and more rigorous estimates with the limited data published previously. Kowalewski et al. (2000) provide data on drilling predation for bivalve mollusks from Permian strata in the Paraná Basin of Brazil, but these are limited only to a few controversial drill holes. They also offered monographic estimates of predation rates on Permian brachiopods of West Texas, based on a series of papers published by Cooper and Grant (1972, 1974, 1975, 1976a, b, 1977). Because we re-examine here bulk materials from which the monographed specimens were acquired, a comparison of monographic estimates of drilling intensity with quantitative bulk estimates will be possible. If reasonable estimates of drilling intensity can be gathered from the literature, then valuable data can be gathered first in the library. This would offer us an effective tool for identifying time intervals and geographic localities most critical for enhancing our understanding of the history of drilling predation.

Finally, the data reported here allow us to compare various metrics used for describing drilling intensity. Drilling intensity can be described from the total of all specimens in an assemblage/sample (e.g., Kelley and Hansen 1993; Kowalewski et al. 1998), by the drilling intensity computed for a selected taxon (e.g., Harper et al. 1998), or by the percentage of taxa that display drill holes (e.g., Vermeij 1987). Nearly

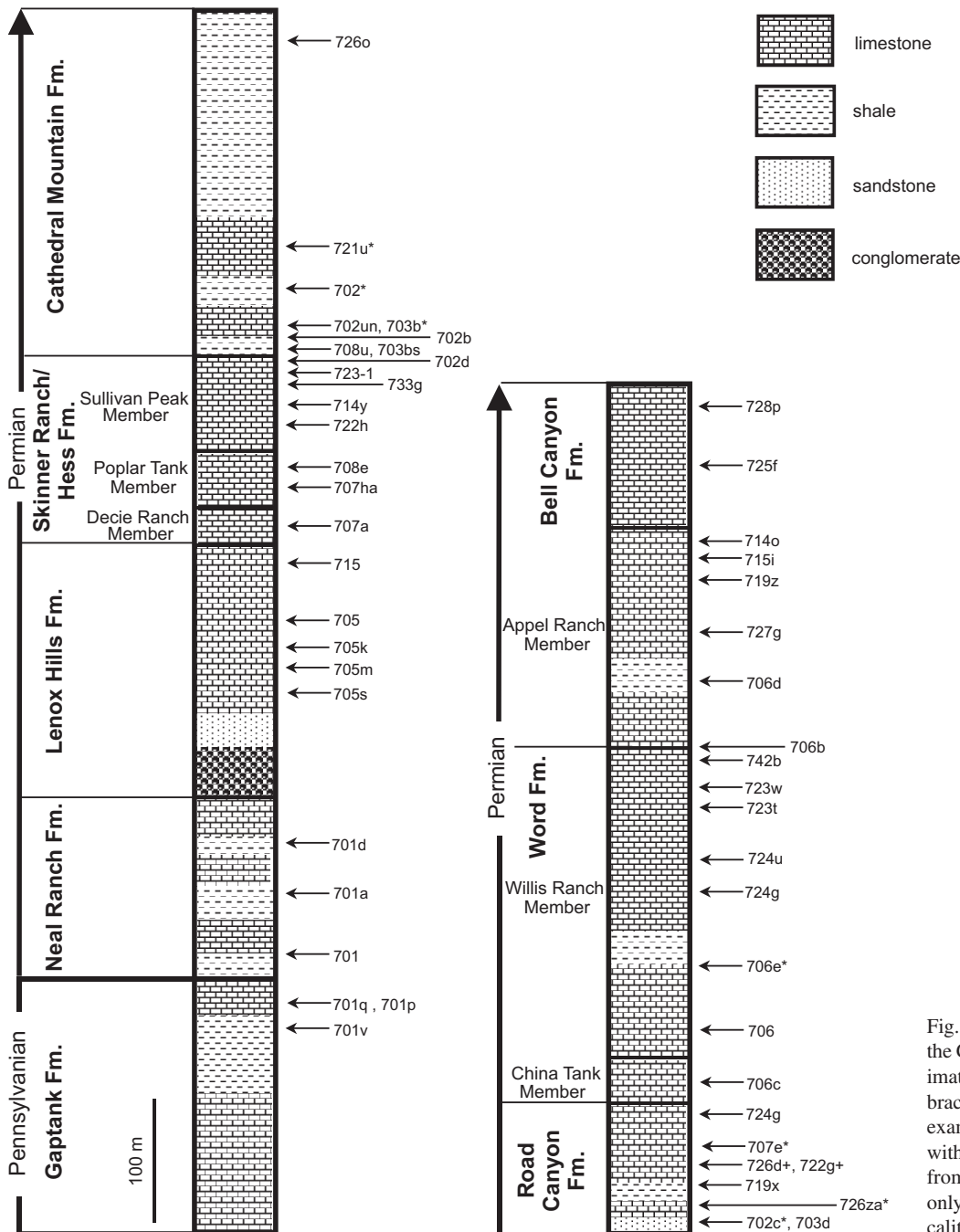


Fig. 2. Composite stratigraphic column of the Glass Mountains area with the approximate location of samples shown. Both brachiopods and bivalve mollusks were examined from sample localities marked with an \*. Only bivalves were examined from localities marked with a +, while only brachiopods were examined from localities indicated just by their number.

all studies of drilling predation to date have employed only one of the metrics to describe drilling intensity, but see Kelley and Hansen (1993) for a study that employed two metrics. Understanding how to best present the data is essential to avoid misrepresenting behavioral, ecological, and evolutionary patterns.

*Depository.*—All material is housed in the Department of Paleobiology at the Smithsonian Institution National Museum of Natural History in Washington, D.C. The acronym for the figured specimens (USNM) stands for United States National Museum.

## Materials and methods

The Glass Mountains have been used as the standard section for the Permian of West Texas because of the completeness of the stratigraphic section in the area (Hill 1996). Rocks in the Glass Mountains span from the upper Pennsylvanian (Gaptank Formation), through the lower Permian (Neal Ranch, Lenox Hills, Skinner Ranch/Hess, Cathedral Mountain, and Road Canyon formations), up into the upper Permian (Word and Bell Canyon formations) (see Hill 1996 for a complete discussion of the stratigraphy of the region). The

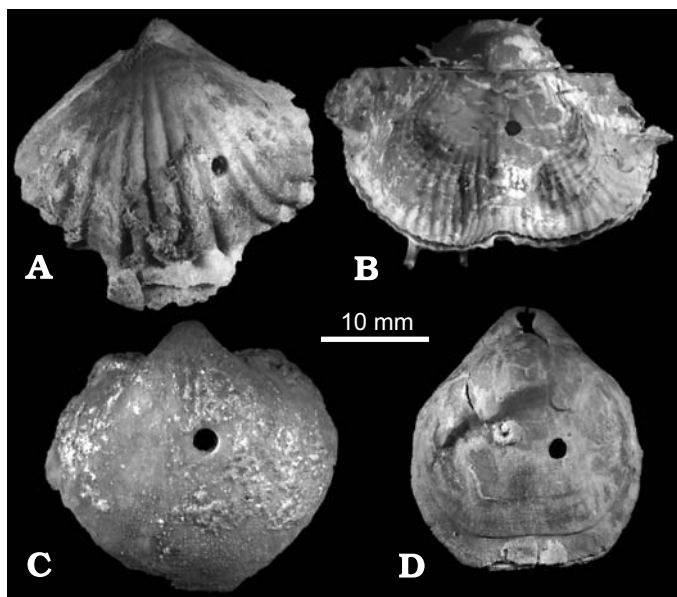


Fig. 3. Drilled brachiopods from the Cooper collection. A. *Stenocisma camurum* (USNM 520070). B. *Kurtoginella umbonata* (USNM 520071). C. *Martinia miranda* (USNM 520072). D. *Composita affinis* (USNM 520073).

section does not include deposits from the latest Permian, and the Permo-Triassic transition is not represented.

G. Arthur Cooper and his colleagues collected limestone blocks from Late Pennsylvanian and Permian strata in the Glass Mountains of West Texas over a period of nearly forty years (Cooper and Grant 1972; Fig. 1). Many of these blocks were shipped to the Smithsonian Institution and subjected to acid dissolution, producing exquisite collections of delicate, silicified fossils from many invertebrate phyla (brachiopods, mollusks (bivalves and gastropods), crinoids, trilobites, and others) (Cooper and Knight 1946). This sampling program generated what is probably the most representative, regional-scale paleontological collection of a sedimentary basin, and provides an ideal opportunity to gather quantitative evidence of drilling predation in the Late Paleozoic. The collections made by Cooper and his colleagues are primarily from the carbonate sediments of the basin and represent environments from shelf break to shallow shelf settings.

Comparing brachiopods to bivalve mollusks is complicated by the fact that the two groups are not taphonomically equivalent. Differences in mineralogy, shell organic content, and mechanical durability may cause differential preservation of those two groups and bias the relative abundance patterns in brachiopod-bivalve assemblages. However, even when such biases are present, the proportions of drilled specimens may still be comparable between brachiopods and bivalves as long as two requirements are met. First, a significant number of specimens must have the original shell material preserved (or replaced) in both groups so that drill holes can be recognized (note that drill holes cannot be reliably detected from molds and casts). In Cooper's collection from the Glass Mountains, shells of both bivalves and brachiopods are preserved through

silicification. Although brachiopods are far more numerous than bivalves, there are enough bivalves present to allow for a statistically reliable comparison of the presence and/or absence of drill holes between the two. Second, the assumption that the preservational effect of drill holes (the mechanical and chemical weakening of the shell induced by the drill hole) is either negligible or exerts a comparable bias in both groups must be made. This assumption is more difficult to evaluate given that experiments with bivalve and brachiopod shells or models do not provide a clear consensus on the taphonomic importance of drill holes (see Roy et al. 1994; Kaplan and Baumiller 2000; Zuschin and Stanton 2001). In particular, there is no data available to compare the effect of compaction on drilled brachiopods and drilled bivalves. This assumption must therefore be considered explicitly when interpreting any comparative results between brachiopods and bivalves.

A conservative estimate of the number of brachiopods recovered by Cooper from the Glass Mountains strata is approximately three million individuals. This incredible number of specimens required a sampling strategy for the collection that would give statistically reliable results in a reasonable period of time. Cooper and Grant (1977) provide a list of species, with relative abundance data for each species, for their sample localities. This compendium was used to select localities to be used in this study. Two criteria were involved in this choice: the stratigraphic position within the section and how many brachiopod genera were listed as common and abundant for those localities (Cooper and Grant 1977 defined common species as being represented by 26 to 100 specimens, abundant species as those represented by 101 to 300 specimens). Localities with at least five common or abundant genera were selected for this study. This did not, however, provide complete stratigraphic coverage, so some localities with less than five common or abundant genera were included to improve stratigraphic completeness (Fig. 2). For each sampled locality, 20 randomly chosen, complete individual specimens from the first species encountered of each common or abundant brachiopod genus were examined for evidence of predatory drilling (in cases where that genus had more than one common or abundant species, the first species encountered was examined in detail and all other species were given a quick visual examination for drilled specimens). The number of specimens examined (20) was selected so that most localities would be represented by at least 100 specimens (at least 5 genera), only localities chosen to fill stratigraphic gaps are represented by fewer than 100 specimens. Whereas other, more complicated strategies for subsampling these collections can be envisioned, the method used here allows for reasonably uniform sampling without requiring an unreasonable amount of time for data collection.

Using the above strategy, drilled specimens from all species of common or abundant brachiopod genera were noted and imaged. All drilled specimens were used when analyzing specimen size versus drill-hole diameter. However, to ensure methodological consistency and uniform sampling intensity across genera that vary in number of abundant species only



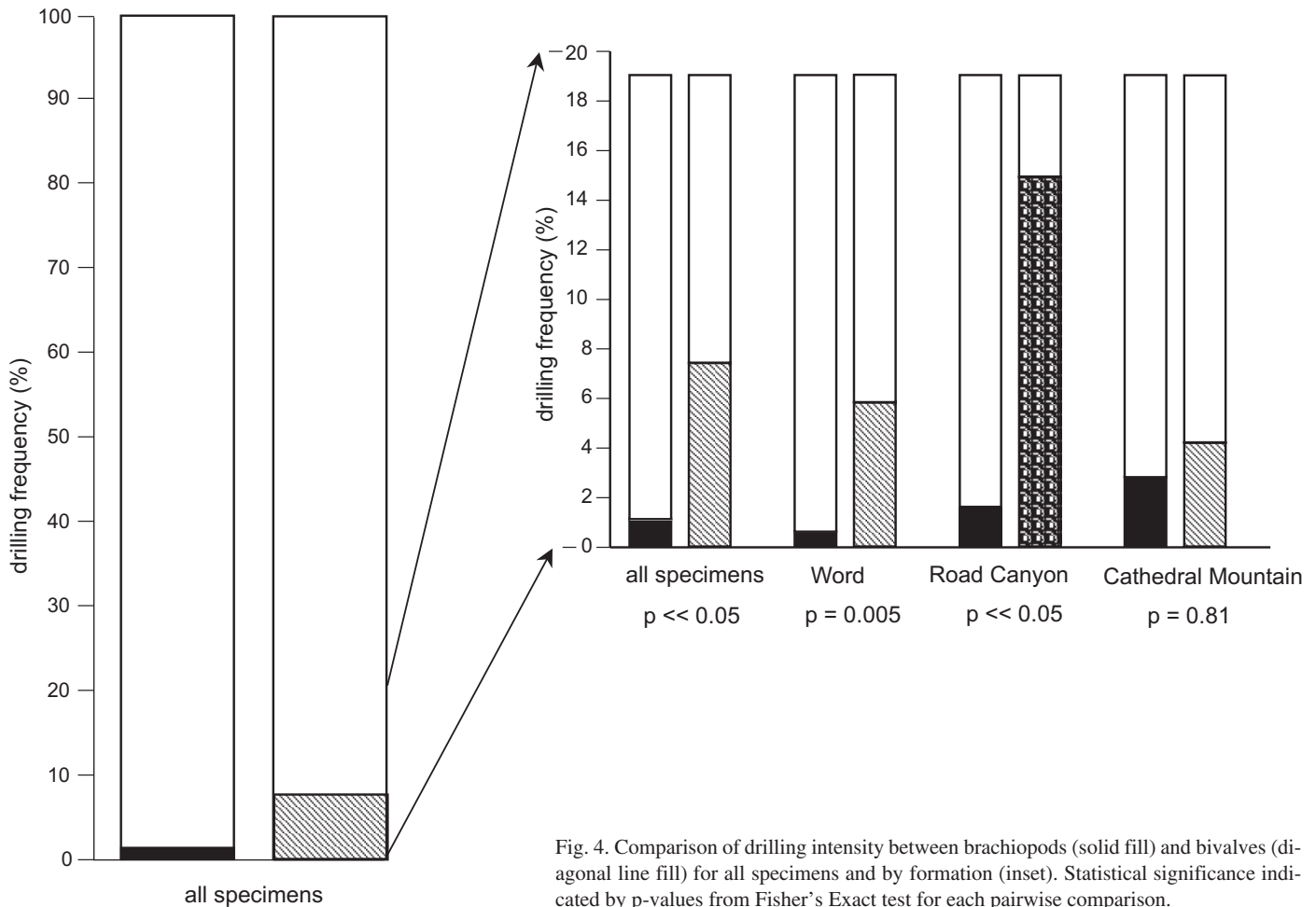


Fig. 4. Comparison of drilling intensity between brachiopods (solid fill) and bivalves (diagonal line fill) for all specimens and by formation (inset). Statistical significance indicated by p-values from Fisher's Exact test for each pairwise comparison.

the first species encountered in the collection was used in the quantitative analysis of drilling frequencies. While the sampling scheme does limit the analysis to only the most common genera, the selected protocol has made this study feasible. More importantly, it is unlikely that rare genera would appreciably alter the results.

Bivalve mollusks are present in far fewer numbers than brachiopods in the collection. This may be a reflection of the difference in abundance between bivalves and brachiopods in the Late Paleozoic, and in fact throughout the Paleozoic (e.g., Gould and Calloway 1980; but see Cherns and Wright 2000). However, a literal interpretation of this difference may not be warranted due to potential taphonomic artifacts (although all specimens are silicified, brachiopods are preserved preferentially, and bivalves may be underrepresented). In addition, the taxonomic resolution of the bivalve specimens was not as complete as that for the brachiopods, indeed many bivalve specimens were not identified beyond noting that they were bivalves. This made it impossible to compare drilling frequencies for bivalves and brachiopods at the genus-level resolution.

The smaller number of bivalve specimens required a different sampling scheme but allowed for a more complete inspection of the specimens available. Rather than limit data

collection to only common and abundant genera, all bivalve species represented by at least five specimens were examined. Unfortunately, the fewer numbers of available bivalves also limit the stratigraphic coverage. Bivalve specimens used in this study represent only the Cathedral Mountain, Road Canyon, and Word formations.

All specimens that displayed definite or potential drill holes were digitally imaged on a scaled black background using a Sony Mavica FD-90 digital camera. These images were used for all measurements to avoid specimen damage. Length, width, and drill-hole diameter were measured for each specimen using Scion NIH software.

Since all of the bivalve specimens examined are preserved as disarticulated valves while most brachiopods are articulated specimens, a correction is required when comparing predation intensities between bivalve mollusks and brachiopods, even though every preserved mollusk valve likely came from a unique individual (Gilinsky and Bennington 1994). This correction must be made because the probability of sampling a drilled valve from a drilled specimen is two times less likely than the probability of sampling any of its two valves (Bambach and Kowalewski 2000; see Hoffmeister and Kowalewski 2001 and Kowalewski 2002, for a thorough explanation of why this is the case).

Table 1. Summary of metrics of drilling intensity. Data for brachiopods only. AI, assemblage drilling intensity; HDT, highest drilled taxon; PT, percent of taxa drilled; NA, not applicable.

Location	Formation	Number of specimens	Number of taxa	AI	HDT	Genus	PT
728p	Bell Canyon	120	6	1.7	10	<i>Composita</i>	16.7
725f	Bell Canyon	60	3	1.7	5	<i>Hustedia</i>	33.3
714o	Word	180	9	0.6	5	<i>Dyoros</i>	11.1
715i	Word	460	23	0.2	5	<i>Glossothyropsis</i>	4.3
719z	Word	480	24	0.4	5	<i>Grandaurispina, Pseudodielasma</i>	8.3
727j	Word	360	18	0	NA	NA	0
706d	Word	120	6	0	NA	NA	0
706b	Word	340	17	0.3	5	<i>Megousia</i>	5.8
742b	Word	160	8	1.3	5	<i>Hustedia, Rhamaria</i>	25
723w	Word	20	1	0	NA	NA	0
723t	Word	220	11	1.4	10	<i>Paucispinifera</i>	18.2
724u	Word	160	8	0.6	5	<i>Cyclacantharia</i>	12.5
724g	Word	20	1	0	NA	NA	0
706e	Word	460	23	0.2	5	<i>Paucispinifera</i>	4.3
706	Word	560	28	0.9	10	<i>Costispinifera</i>	14.3
706c	Word	320	16	0.9	10	<i>Liosotella</i>	12.5
724j	Road Canyon	40	2	0	NA	NA	0
707e	Road Canyon	220	11	2.3	10	<i>Stenocisma, Rhynchopora</i>	45.4
719x	Road Canyon	140	7	0	NA	NA	0
726za	Road Canyon	40	2	12.5	25	<i>Composita</i>	50
703d	Road Canyon	20	1	0	NA	NA	0
702c	Road Canyon	340	17	0.6	5	<i>Echinauris, Kurtoginella</i>	11.7
726o	Cathedral Mtn	220	11	0	NA	NA	0
721u	Cathedral Mtn	220	11	4.5	20	Composita	45.4
702	Cathedral Mtn	340	17	3.2	15	<i>Composita, Martinia, Stenocisma</i>	29.4
702un	Cathedral Mtn	240	12	1.6	10	<i>Meekella, Rugatia</i>	16.6
703b	Cathedral Mtn	80	4	1.3	5	<i>Nudauris</i>	25
702b	Cathedral Mtn	300	15	4.7	35	<i>Martinia</i>	53.5
708u	Cathedral Mtn	20	1	0	NA	NA	0
703bs	Cathedral Mtn	40	2	0	NA	NA	0
702d	Cathedral Mtn	40	2	0	NA	NA	0
723-l	Skinner Ranch	40	2	0	NA	NA	0
733j	Skinner Ranch	120	6	0	NA	NA	0
714y	Skinner Ranch	100	5	0	NA	NA	0
722h	Skinner Ranch	180	9	0	NA	NA	0
708e	Skinner Ranch	60	3	0	NA	NA	0
707ha	Skinner Ranch	120	6	0	NA	NA	0
707a	Skinner Ranch	40	2	0	NA	NA	0
715	Lenox Hills	20	1	0	NA	NA	0
705	Lenox Hills	20	1	0	NA	NA	0
705k	Lenox Hills	60	3	0	NA	NA	0
705m	Lenox Hills	20	1	0	NA	NA	0
705s	Lenox Hills	20	1	0	NA	NA	0
701d	Neal Ranch	180	6	0.6	5	<i>Hustedia</i>	11.1
701a	Neal Ranch	20	1	0	NA	NA	0
701	Neal Ranch	120	9	1.7	5	<i>Hustedia, Meekella</i>	33.3
701q	Gaptank	89	5	0	NA	NA	0
701p	Gaptank	11	2	0	NA	NA	0
701v	Gaptank	37	1	0	NA	NA	0

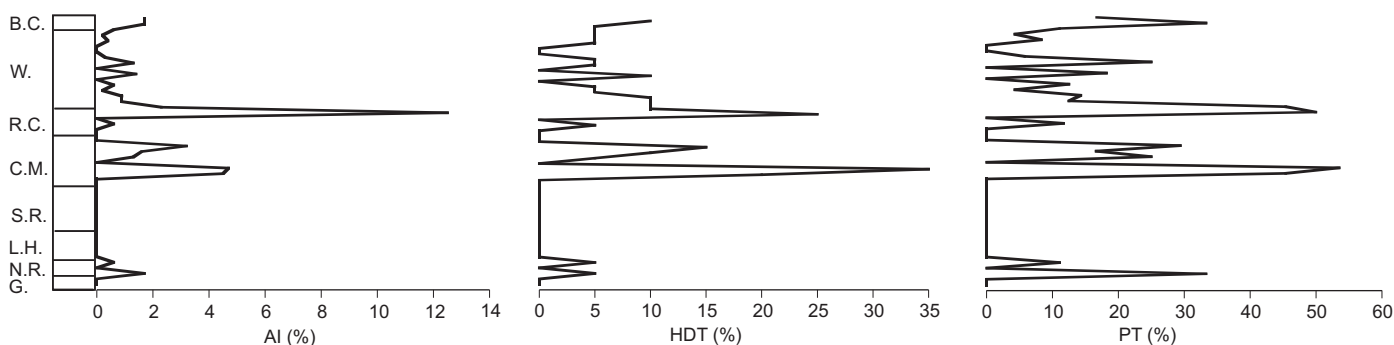


Fig. 5. Temporal distribution of drilling predation using three different metrics. AI, assemblage drilling intensity; HDT, highest drilled taxon; PT, percent of taxa drilled. See Fig. 2 for full formation names.

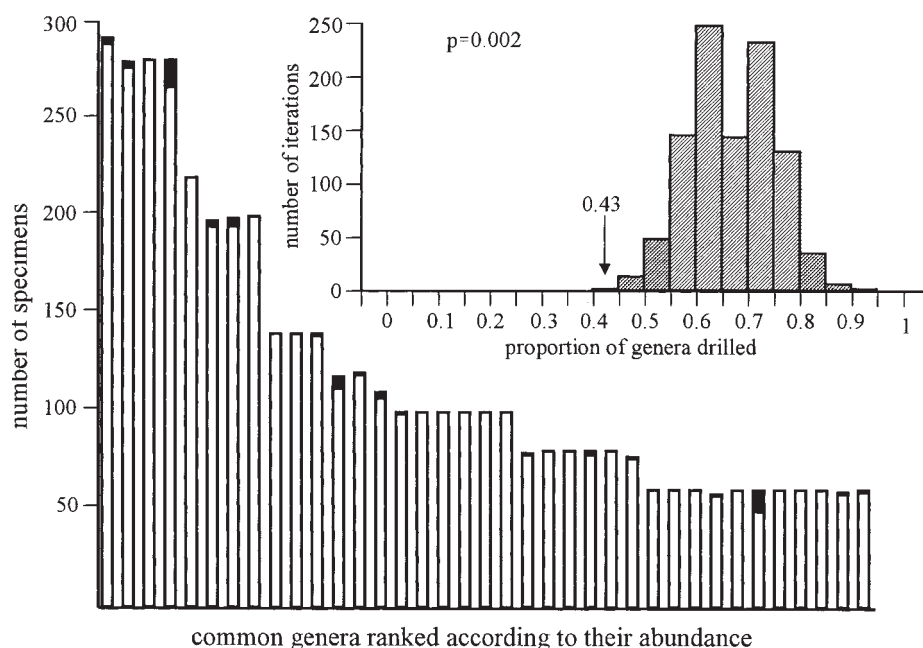


Fig. 6. Genus selectivity in drilling on Permian brachiopods from West Texas for genera represented by at least 50 individuals. Each bar represents a single genus, the white section of the bar represents specimens that are not drilled and the black section at the top of the bar, when present, indicates drilled specimens. Inset shows the results of a Monte Carlo simulation, using the actual drilling intensity and distribution of genera from the data. The results indicate that the selection of brachiopod prey/host is non-random.

In this study we use the following criteria to define a drill hole: (1) the hole is circular or oval, and unhealed, (2) the hole is perpendicular to the shell, (3) the hole penetrates only one valve of articulated specimens, and (4) the hole likely penetrates the valve from the outside (i.e., the outer hole diameter exceeds the inner hole diameter). These criteria should exclude holes made by substrate borers or by abiotic dissolution processes, but may result in the inclusion of both parasitic (i.e. including also parasitism of the food source, and parasitism of the tissue of the host) as well as lethal predatory drill holes.

To avoid confusion with respect to which metric is being discussed we employ the following terminology. Assemblage drilling intensity (AI), calculated for data pooled across all taxa included in the sample, is computed as the number of drilled specimens divided by the total number of specimens,

again including any corrections needed (see above). Highest drilled taxon intensity (HDT) is calculated as the number of drilled specimens in the most frequently drilled lower taxon (genus in this study) divided by the total number of specimens from that taxon, again including any corrections needed. Percent taxa drilled intensity (PT) is calculated as the total number of taxa (genera) that display drill holes divided by the total number of taxa examined. Results from all calculations are reported as percent values. Each of these metrics may be calculated at the sample level, formation level or for all specimens.

Statistical analyses were performed using Statistical Analysis System version 8 using a significance criterion of 5% ( $\alpha = 0.05$ ). In case of multiple independent tests, the Bonferroni correction ( $\alpha_B = \alpha/\#$  tests) was applied and the corrected  $\alpha_B$  was used to make statistical decisions. The analyses were done using codes written in SAS and SAS/IML.

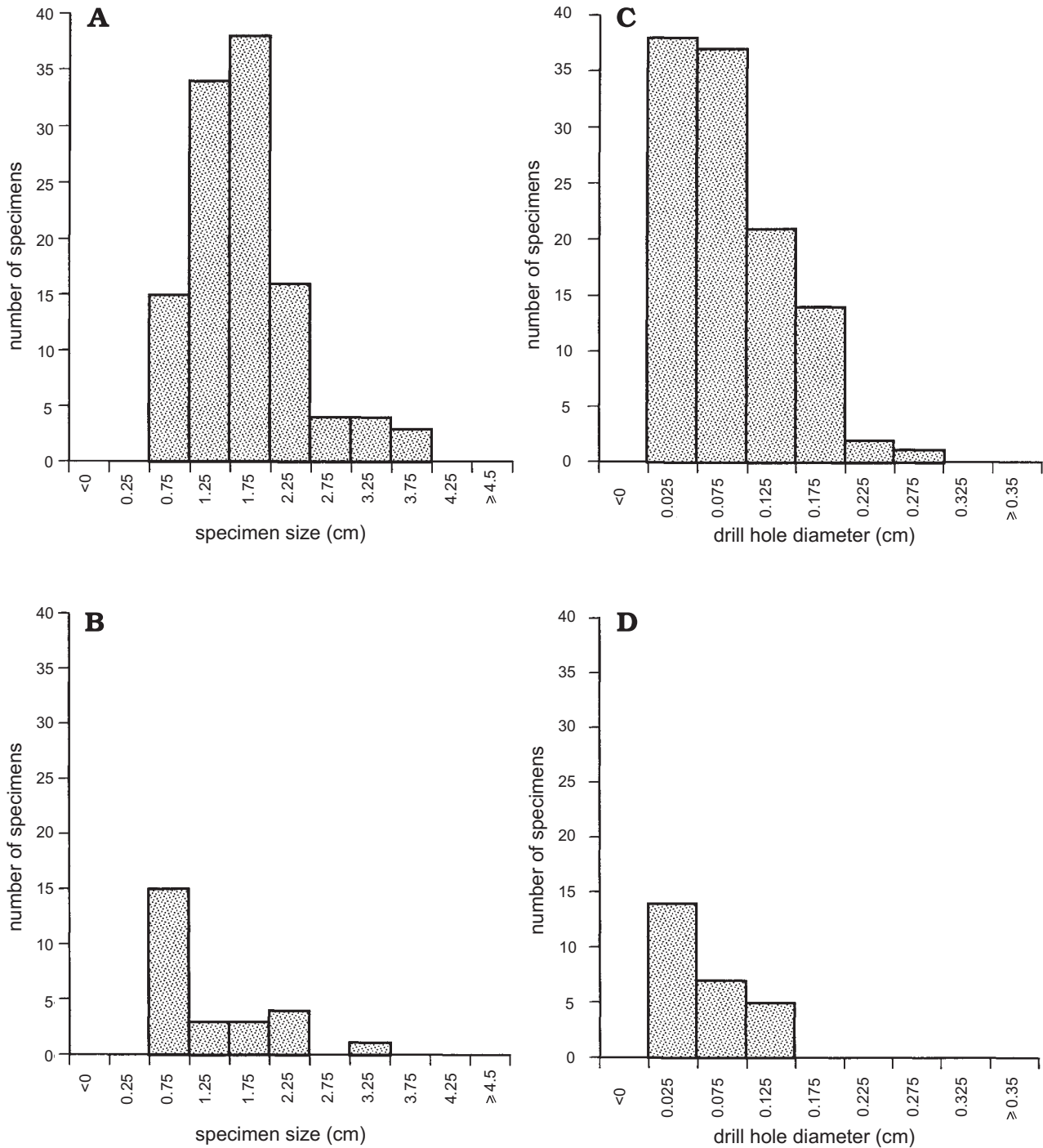


Fig. 7. Size frequency distributions for drilled prey shells and drill holes for: **A**. Drilled brachiopod specimens. **B**. Drilled bivalve mollusk specimens. **C**. Drill holes in brachiopods. **D**. Drill holes in bivalve mollusks.

## Results

The drill holes encountered in the examined brachiopods and bivalve mollusks range in shape from circular to sub-circular. The majority of the penetrations do not display a beveled edge (see Fig. 3), although there are cases where distinct beveling, similar to that produced by naticid gastropods in modern settings, is present. There is no consistent pattern of asso-

ciation with respect to the shape of the drill hole in plan view and the presence of a beveled edge. Anterior-posterior length in brachiopod specimens ranges from 6.1 mm to 39.1 mm (mean = 16.6 mm). For bivalve mollusk specimens, anterior-posterior length ranges from 5.1 mm to 34.1 mm (mean = 11.9 mm). Drill hole diameter ranges from 0.1 mm to 2.6 mm (mean = 0.8 mm) in brachiopod specimens, while in bivalves the drill hole diameter ranges from 0.1 mm to 1.4 mm (mean = 0.5 mm).



7597 brachiopod specimens were examined from 48 sample localities. Of these, 81 specimens display drill holes of a predatory/parasitic nature (drilling intensity of 1.07%) and an additional 30 specimens display drill holes that are more questionable (drilling intensity is 1.46% when questionable holes are included; Table 1). Sample-level assemblage frequencies (AI) for brachiopods ranged from 0 to 12.5%; while HDT ranges from 5 to 35% and PT ranges from 0% to 53.5% (see Table 1).

619 bivalve mollusk specimens represented exclusively by disarticulated valves were examined from 9 sample localities. 23 valves display definite drill holes (drilling intensity of 7.43%;  $23/(619 \times 0.5)$ ) and another 5 specimens display drill holes that are more questionable (drilling intensity of 9.05% if included).

There may be a preference for bivalve mollusks as prey/host over brachiopods when all specimens are considered together (AI = 7.43% vs. 1.07%, Fisher's Exact Test  $p \leq 0.05$ ; Fig. 4). This apparent preference is generally seen within individual stratigraphic units that yielded sufficient numbers of bivalves for a quantitative comparison. In all three cases, drilling intensity in bivalves is higher than in brachiopods, and in two of these cases the difference is significant statistically ( $p < 0.01$ ;  $\alpha_B = 0.017$ ; see Fig. 4).

Values for all metrics of drilling predation vary among samples both spatially and temporally. Spatially there is no clear pattern across different localities (Cooper and Grant 1972, provided location maps for many of the sample localities used in this study). In many cases, adjacent localities representing the same stratigraphic units included both sites that yielded numerous drilled specimens as well as sites that did not produce even a single drilled fossil.

Each of the three metrics employed (AI, HDT, PT) can be used to investigate temporal trends in drilling intensity. Because of the scarcity of bivalves, this analysis is limited to brachiopods. There is a remarkable similarity between the plots (Fig. 5). The lower part of the section (Gaptank Formation to Skinner Ranch Formation) is characterized by the general absence of drilled specimens, with only the Neal Ranch Formation containing evidence of drilling predation. The Cathedral Mountain and Road Canyon formations display the highest values for each metric. It is interesting to note that while the Road Canyon Formation has the highest AI value for all specimens (Fig. 5), the highest HDT and PT values are in the Cathedral Mountain Formation (Fig. 5). Another notable difference among metrics is the suggestion of a third peak in the Bell Canyon Formation for PT that is not as clearly expressed in the other two plots.

The taxonomic distribution of drilled specimens analyzed for common brachiopod genera ( $n = 4452$ ) shows that out of 37 brachiopod genera represented in the data by at least 50 specimens, 16 genera are drilled (PT = 43.2%). Drill holes tend to be rare (AI = 1.1%) so many genera do not include any specimens with traces (Fig. 6). It is not immediately clear if this pattern of drill-hole distribution is non-random across the genera. To assess this issue a Monte Carlo simulation was

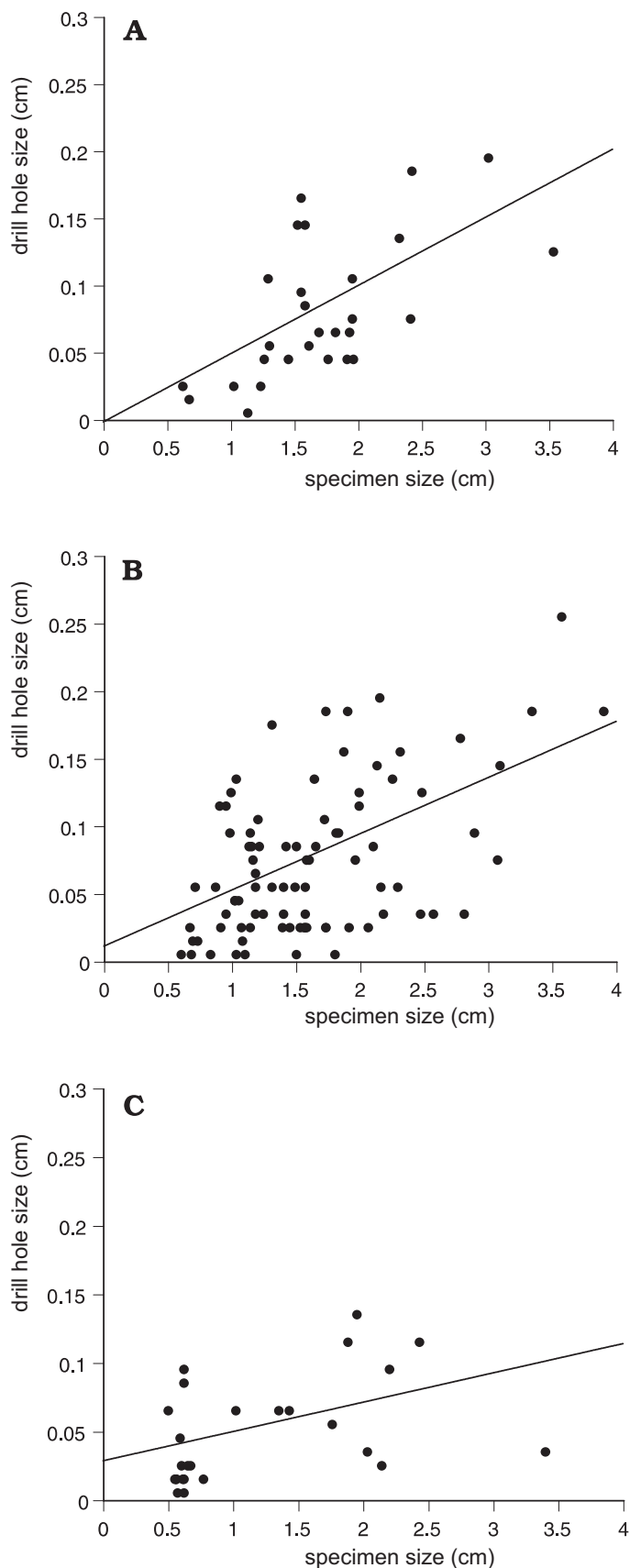


Fig. 8. Plots of specimen size versus drill-hole diameter. **A.** Brachiopods with drill holes in the pedicle valve. **B.** Brachiopods with drill hole in the brachial valve. **C.** All bivalve specimens.

used to draw random samples of 4452 specimens assigned to 37 genera of brachiopods, mimicking the actual sample sizes for those genera. The simulated specimens were then “drilled” by the computer with an a priori assigned probability of 1.1%. The inset plot shows the result of the simulation. Only one time in 999 iterations was the simulated PT value lower than or equal to 43.2%, demonstrating that drill holes are distributed non-randomly (i.e., if drilling was random, significantly more genera should contain holes than observed). The reported  $p = 0.002$  includes 999 random values and the actual sample (see Manly 1997).

The size-frequency distributions for brachiopod and bivalve mollusk specimens are visually similar to the size frequency distribution of the drill holes seen in each (Fig. 7). The ranges of both specimen and drill hole size are larger for brachiopods than for bivalves, but while the specimen size distributions are significantly different (Kolmogorov-Smirnov test  $p < 0.05$ ), the distributions of drill hole size do not differ significantly (Kolmogorov-Smirnov test  $p = 0.19$ ). There is no clear relationship between specimen size and drill-hole diameter in either brachiopods or bivalves (Fig. 8).

Finally, there also seems to be a preference for drilling in the pedicle valve of brachiopods. Of 81 drill holes, 57 (70.4%) are in the pedicle valve (Fisher’s Exact Test,  $p \leq 0.05$ ).

## Discussion

It seems clear that predators and/or parasites with the ability to drill through hard shells were present throughout the Permian (Kowalewski et al. 2000; this study). The data presented here indicate that drilling intensity may have been higher than that reported by Kowalewski et al. (1998), especially for bivalve mollusks. However, this higher drilling intensity is still significantly lower than the levels seen in the Late Mesozoic and Cenozoic. This supports the idea that drilling intensity in benthic marine ecosystems generally remained low throughout the Paleozoic and did not increase until some time in the Mesozoic.

When all specimens are considered together, bivalve mollusks appear to be the preferred prey and/or host (drilling intensity of 7.43% vs. 1.07%,  $p \leq 0.05$ ), which is particularly notable given the lower abundance of bivalves. This preference may suggest that Late Paleozoic drillers had recognized which prey/host would provide the most return for the effort of attack (Peck 1993). If this interpretation is correct, then drill holes are more likely to record predators, and not parasites.

However, other explanations can account for this preferential pattern. First, the difference may reflect differences in life habit. Brachiopods are epifaunal, whereas the bivalves included in our samples, include both epifaunal and infaunal forms. If the driller was infaunal, then bivalves would be encountered more often and thus be subject to drilling more frequently. There are not enough drilled specimens of bivalves with reliably established mode of life (epifaunal vs. infaunal) to adequately test this idea. However, the presence of many

drilled brachiopods indicates that drillers were able to access and attack brachiopods (perhaps by mistake; e.g., Walker and Yamada 1993), and thus, the “infaunal driller” scenario is not very likely. Second, the preference may reflect the fact that drilling organisms occur preferentially in environments where bivalves are more common and/or brachiopod more scarce. However, the fact that brachiopods are sometimes drilled at high frequencies indicates that the preference for bivalves is not a spurious result of drillers unable to access brachiopods. Moreover, brachiopods and bivalves co-occur in the same units, and whenever they do, bivalves are always drilled at higher frequencies than brachiopods. Finally, the preference may be a taphonomic artifact. If drill holes lower the preservational potential of the brachiopods and bivalves to a different degree, the proportion of the preserved drilled specimens may be suppressed to a higher degree in one of those two taxa. However, given that bivalves analyzed here tend to be smaller and more fragile than brachiopods, it is more likely that the data are biased in favor of brachiopods; that is, the higher frequency of drilling observed in bivalves is preserved despite a possible preservational bias against them. Thus, despite all caveats, there is a distinct possibility that drillers preferentially selected bivalves over brachiopods. They attacked bivalves when those were readily available, but switched to brachiopods when bivalves were rare.

The apparent preference in prey observed at the genus level within brachiopods is also strongly supported by the Monte Carlo simulation performed for the distribution of drilling in brachiopods by genera. The actual value for the proportion of genera drilled gathered from the data is much lower than what would be expected if the drillings were randomly distributed. Some brachiopod genera were, it seems, preferentially chosen for attack, although the reason for this selection is not yet clear. However, it is possible that the apparent preference seen in the data is the result not of selectivity on the part of the predator but of temporal mixing (time averaging). For example, if prey species from two times are mixed, and predators were only present at one of these times, then some proportion of the total suite of prey species would never have come into contact with the predator and therefore would never show any effects of predation. This mixing can have two effects; first, it could lower the overall drilling intensity for the bulk collection and second, it could make some prey species appear to be preferred over others.

The apparent lack of any meaningful spatial pattern in the distribution of drilling predation/parasitism in the Glass Mountains strata is not entirely unexpected. The samples were all collected from rocks representing similar depositional environments and facies. This does not preclude the possibility that significant differences exist between the siliciclastic and carbonate parts of the section, but at this time we know of no collections that would allow for comparison of this nature.

Spatial variation in drilling predation/parasitism during short time spans in the Cenozoic has been shown to be as extensive as the variation seen throughout the Cenozoic (Hansen and Kelley 1995; Hoffmeister and Kowalewski 2001). It is

therefore not surprising that we see significant spatial variation in the Paleozoic as well. Both migration of predators through space and time and the patchy nature of the fossil record will influence the observed spatial distribution of drilling predation.

The pattern of drilling predation/parasitism through the Paleozoic seems to be more complex than previously reported. While the intensity of drilling in brachiopods from the Permian of West Texas is quite low compared to reports of brachiopod predation in the Devonian (e.g., Smith et al. 1985; Leighton 2001), the intensity seen in the Permian bivalves is very similar to the intensities reported for Devonian brachiopods. Unfortunately, we know of no studies of predation on Devonian bivalves so a direct comparison of time intervals for bivalves cannot be accomplished.

One unexpected result is a large stratigraphic interval within which none of the samples contain drill holes. The Lenox Hills and Skinner Ranch formations contained a total of twelve localities and 800 specimens without a single drilled specimen. Predators/parasites with the ability to drill likely existed during this time since there is evidence of drilling in the older Neal Ranch Formation and in all of the younger formations. The lack of drilled specimens cannot be ascribed to poor recovery from the carbonate blocks. It is possible that either drilling frequencies were very low (i.e., rare enough to be missed when the individual specimens chosen at random for this study were selected) or drillers were temporarily absent due to temporal changes in their geographic ranges.

The comparison of drilled bivalve mollusks reported here with the Permian bivalves reported from southern Brazil by Kowalewski et al. (2000) shows notable differences. Bivalve mollusks from the Permian of West Texas have a significantly higher drilling intensity (7.4%) than those reported from the Paraná Basin in Brazil (less than 1%) (Fisher's Exact test  $p \leq 0.05$ ). Several factors are likely the cause of this disparity. First, the Paraná Basin may have been affected by brackish conditions, at least intermittently, during Permian times (see Simões and Kowalewski 1998) and, consequently, drilling organisms may have been absent (most of the present-day drilling predators and parasites are exclusively marine). Also, the West Texas material displays a greater degree of silicification than that seen from Brazil. First, much of the Brazilian assemblage is preserved as internal molds, which makes it virtually impossible to recognize drill holes with any confidence. Second, silicification in the Brazilian assemblage is not uniformly distributed; some patches are highly silicified while others are not. This certainly affects the composition of the assemblage and may affect the observed drilling intensity as well.

The estimates of drilling frequency for brachiopods from West Texas derived from monographic literature (0.5% to 1%; Kowalewski et al. 2000) are similar to, although somewhat lower than, those reported here (1.07%). While the difference between the definite drilling intensities (0.5%, Kowalewski et al. 2000; 1.07%, this study) is significant (Fisher's Exact Test,  $p \leq 0.05$ ), the lower estimate provided by the monographic literature is comparable in magnitude and did provide a reasonable first approximation, correctly revealing that drilled speci-

mens were very infrequent. This is a promising result. The logical preference in choosing specimens for illustration is to select the most perfect individuals possible, which would almost always preclude drilled specimens. However, in this case it seems that the authors were equally concerned with presenting a complete account of the fauna. If this attention to detail is consistent among various monograph authors, then careful examination of monographic literature should provide a reasonable initial estimate of drilling predation throughout the Paleozoic and help to identify periods of time and localities where additional field collections would be most fruitful.

The three metrics used to describe drilling predation (AI, HDT, PT) produced remarkably similar results. Data published by Kelley and Hansen (1993) also generate plots for drilling intensity and percent taxa drilled that are similar. This similarity in results provides an indication that there is some relationship between the metrics such that which one is chosen may not be a critical issue. However, it is premature to draw any far-reaching conclusions based on these two case studies only; that is, the similar behavior of the metrics seen here need not hold true for other case studies.

The data presented here show unexpected complexity in the temporal and spatial distribution of Paleozoic drilling. Clearly, much work still needs to be done to completely understand the pattern of drilling predation in the Paleozoic. In particular, the paucity of data regarding drilling predation on Paleozoic (and Mesozoic) bivalves hampers our current understanding of the evolutionary history of drilling behavior. The most efficient manner of acquiring the needed data may be to (1) examine monographic literature regarding Paleozoic brachiopods and mollusks, (2) re-examine the bulk collected material used in the monographs, (3) examine any additional bulk collected materials available in museums and universities, and (4) use the results to acquire new bulk collections that will effectively fill in temporal gaps in the fossil record of drilling behavior. Quite likely, new bulk collections will be needed from all periods of the Paleozoic to accurately depict the development of drilling predation throughout the Paleozoic and the role that this behavior played in the evolution of brachiopods and bivalve mollusks.

This research has, for the first time, provided definite evidence for drilling predation/parasitism on bivalve mollusks in the Late Paleozoic. We have documented that both brachiopods and bivalves, living in the same environment, were subject to drilling predation/parasitism in the Late Paleozoic. Our data indicate that bivalve mollusks from Permian strata in West Texas experienced a higher drilling intensity than brachiopods obtained from the same samples, possibly indicating preferential drilling of bivalves over brachiopods already in the Paleozoic.

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