Intense drilling in the Carboniferous brachiopod *Cardiarina cordata* Cooper, 1956

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The brachiopod *Cardiarina cordata*, collected from a Late Pennsylvanian (Virgilian) limestone unit in Grapevine Canyon (Sacramento Mts., New Mexico), reveals frequent drillings: 32.7% ($n = 400$) of these small, invariably articulated specimens (<2 mm size) display small (<0.2 mm), round often beveled holes that are typically single and penetrate one valve of an articulated shell. The observed drilling frequency is comparable with frequencies observed in the Late Mesozoic and Cenozoic. The drilling organism displayed high valve and site selectivity, although the exact nature of the biotic interaction recorded by drill holes (parasitism vs. predation) cannot be established. In addition, prey/host size may have been an important factor in the selection of prey/host taxa by the predator/parasite. These results suggest that drilling interactions occasionally occurred at high (Cenozoic-like) frequencies in the Paleozoic. However, such anomalously high frequencies may have been restricted to small prey/host with small drill holes. Small drillings in *C. cordata*, and other Paleozoic brachiopods, may record a different guild of predators/parasites than the larger, but less common, drill holes previously documented for Paleozoic brachiopods, echinoderms, and mollusks. ☐ *Brachiopod, Carboniferous, drilling, parasitism, predation.*

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Intense drilling predation (>20%) is a common phenomenon in Late Mesozoic and Cenozoic molluscan fossil assemblages (e.g. Hoffman & Martinell 1984; Vermeij 1987; Kelley & Hansen 1993, 1996; Hoffmeister & Kowalewski 2001). In contrast, the drilling frequencies documented to date for Paleozoic assemblages, mainly for brachiopod prey/host, rarely exceed 10%.

Although drilling predation/parasitism on brachiopods has been documented for all periods of the Paleozoic, the reported levels of drilling intensity are low (typically less than 1%) (Cameron 1967; Buehler 1969; Rohr 1976; Ausich & Gurrola 1979; Miller & Sundberd 1984; Chatterton & Whitehead 1987; Conway Morris & Bengtson 1994; Kowalewski *et al.* 1998, 2000; Kaplan & Baumiller 2000). Only a few studies have reported occurrences where the frequency of drilling on brachiopods exceeds 10% (Brunton & Champion 1974; Smith *et al.* 1985; Baumiller *et al.* 1999; Leighton 2001). This generally low frequency of predation may be related to the energy budget of the predator (low nutrient gain from the prey; see Kitchell *et al.* 1981), the lifestyle of the predator (drilling may have been facultative), the low relative abundance of the predator, or some form of defense and/or toxicity of brachiopod prey (Thayer 1985). Whatever the reason, it is clear that high frequencies of drilling predation (>10%) on brachiopods are rarely observed in the Paleozoic, both for the entire assemblage and for individual taxa.

As part of a comprehensive investigation of drilling predation on Paleozoic brachiopods, bulk collected material housed in museums has been searched for evidence of drilling predation. In particular, we focused on enormous collections made by the late G. Arthur Cooper. The collections are housed in the Smithsonian Institution, Washington D.C. and provide an excellent starting point for exploratory analyses of rare events such as drill holes in Paleozoic brachiopods. We present a case study documenting

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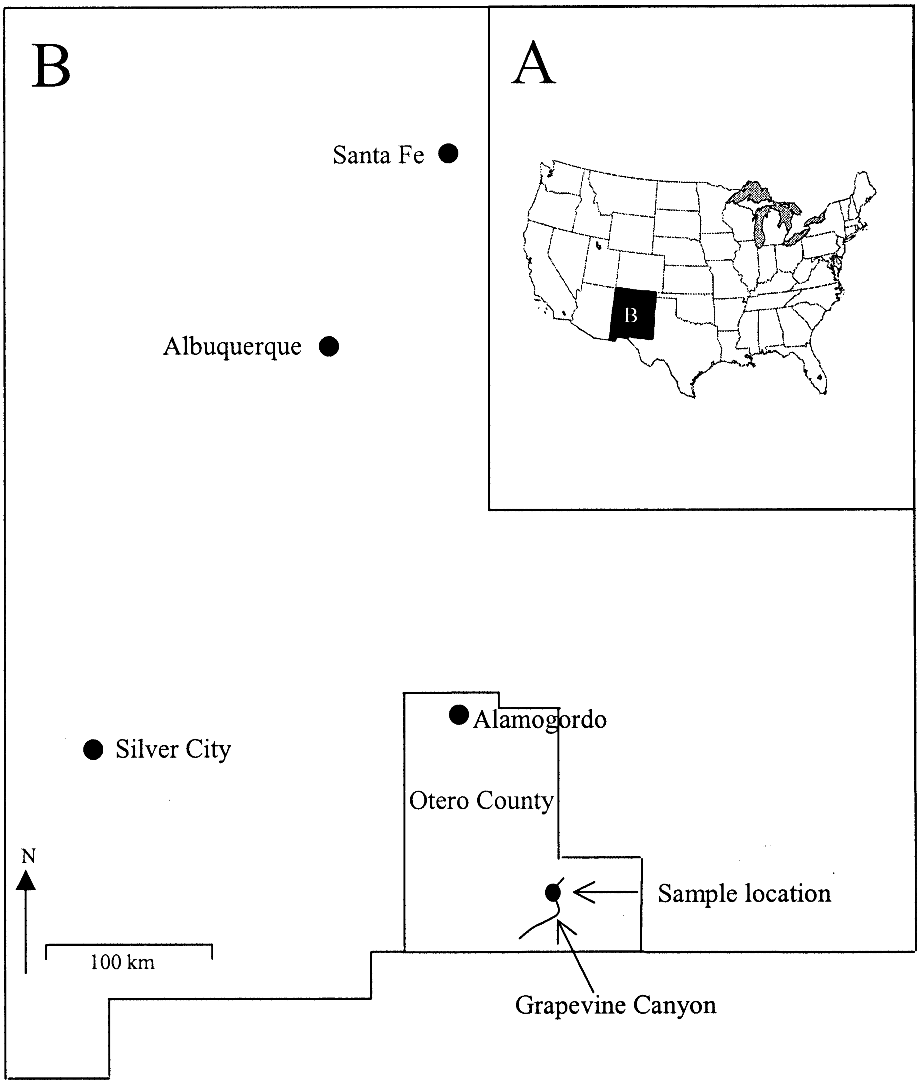

Fig. 1. Study area. □A. Map of the United States with New Mexico shaded in black. □B. Map of the state of New Mexico showing the location of Grapevine Canyon in Otero County.

intense drilling predation in the Late Paleozoic, with a drilling frequency comparable to frequencies that, to date, have only been observed in the Cenozoic.

Materials and methods

Cooper (1956) described three small brachiopod species from the Magdalena Group in the Sacramento Mountains, Otero County, New Mexico: *Coledium* (*Stenocisma*) *bowsheri* Cooper, 1956, *Oligothyrina alleni* Cooper, 1956, and *Cardiarina cordata*, Cooper 1956. When describing *C. cordata* Cooper (1956, p. 529) stated that ' … many of the specimens bear a small round hole located in any part of the exterior except the beak. This small hole suggests a gastropod boring'. One of the specimens figured by Cooper (1956, plate 61, fig. 1) shows a prominent hole in the dorsal valve. The hole is circular, perpendicular to the shell and only penetrates one valve. These are all characteristics that typify predatory/parasitic borings (note that parasitism in this case likely involves parasitism of the host's food source not an infection of the host organism). No mention was made of drill holes in the other two species. The only other report of possible drilling predation in a Pennsylvanian brachiopod known to the authors is by Hoare & Atwater (1980) on the brachiopod *Composita* from the Vanport Shale of Ohio. Since there are so few reports of drilling predation from Pennsylvanian strata in the literature, we revisited Cooper's collection to investigate possible evidence for drilling predation in *C. cordata* in detail.

Otero county is located in the south-central section of New Mexico. The site where Cooper (1956) sampled the Magdalena Group is in the upper part

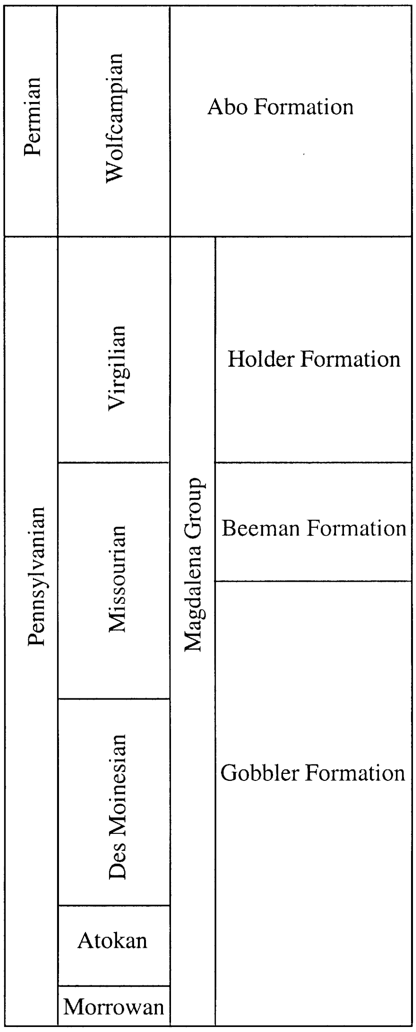

Fig. 2. Generalized stratigraphic column of Pennsylvanian and earliest Permian units in the Sacramento Mountains of New Mexico. Specimens for this study come from the upper part of the Holder Formation.

of Grapevine Canyon, in the Sacramento Mountains located within the Lincoln National Forest, southeast of the city of Alamogordo (Fig. 1). It should be noted that when Cooper published his paper, the studied unit had the status of a formation. Subsequently, the Magdalena Formation has been raised to group status (Fig. 2), and, in New Mexico, split into three formations (Keroher *et al.* 1966). Cooper's samples come from a single, ledge-forming limestone bed near the top of what is now the Holder Formation (Late Pennsylvanian (Virgilian) in age). Samples that encompass the entire 23–30 cm thick limestone ledge were collected, subjected to acid dissolution and all fossils were recovered from the siliceous residue.

All specimens of *C. bowsheri, O. alleni*, and *C. cordata* from the Magdalena Group were acquired on loan from the Smithsonian Institution National Museum of Natural History (SINMNH), Washington, D.C. Each specimen was examined and measured under a Bausch and Lomb binocular microscope with magnification ranging between 10× and 30×. Anterior-posterior measurements were made using millimeter-scale engineering paper. Multiple measurements of a random subset of specimens produced results repeatable to the nearest 0.1 mm. All drilled specimens were digitally imaged using a Nikon Coolpix 990 digital camera attached to a Nikon petrographic microscope with an external fiber optic light source. The vast majority of specimens examined (>90%) comprise complete, articulated shells. All drilled specimens are articulated. Complete disarticulated valves and shell or valve fragments sufficiently complete to estimate their dimensions were also included in the size analysis.

Following a strategy proposed by Roopnarine & Buessink (1999), landmark methods were used to evaluate site selectivity of drilling. Data were collected for all *C. cordata* specimens with single drill holes (95% of the drilled specimens). X-Y coordinates of the center of the drill hole and four landmarks were acquired digitally. The landmarks, the tip of the beak, the point of maximum invagination between the two lobes, and the point of maximum curvature for each lobe, are used here. These landmarks are geometrically defined and may not be biologically valid (homologous) landmarks. However, these pseudo-landmarks serve here primarily as geometric reference points to quantify the position of drill holes and standardize specimens in terms of orientation, position, and size.

The landmark data were transformed into shape (Bookstein) coordinates by a process of translation, rotation, and reorientation with respect to a common baseline (for more details, see Bookstein 1991; Foote 1991). The reference baseline was defined by the tip of the beak and the point of maximum invagination between the lobes. This process minimizes variation due to size differences in the specimens. A uniform grid was generated and the shape coordinates of the points of maximum curvature for each lobe were plotted with respect to the common baseline. An outline of *C. cordata* was then placed on the grid using the endpoints of the baseline as anchors. Shape coordinates of the drill holes were also plotted on the grid with respect to the common baseline. By calculating the frequency of drill holes in any grid square (see also Reyment 1971; Kowalewski *et al.* 1997; Roopnarine & Buessink 1999), stereotypy in drill-hole location for each valve was assessed. Statistical analyses were performed using Statistical Analysis System version 8. All statistical analyses were performed using a significance criterion of 5% ($\alpha = 0.05$). The analyses were done using SAS codes written by the authors.

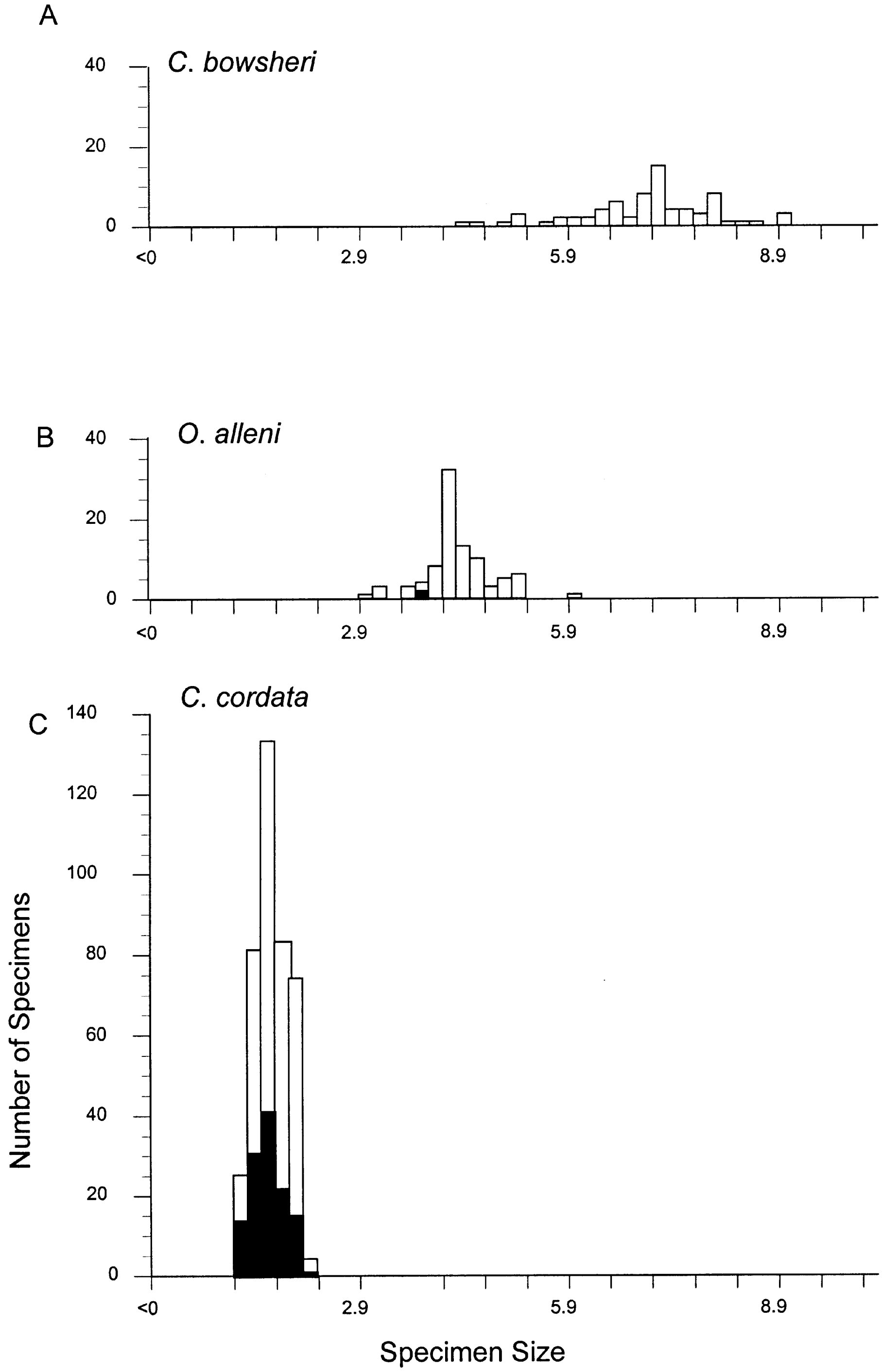

Fig. 3. Size distributions for the three species described by Cooper (1956). □A. *Coledium bowsheri.* □B. *Oligothyrina alleni.* □C. *Cardiarina cordata.* Filled sections of the bars indicate drilled specimens, open sections indicate specimens without drill holes.

Results

The data consists of 562 specimens: 73 of *Coledium bowsheri*, 89 of *Oligothyrina alleni*, and 400 of *Cardiarina cordata*. These numbers represent all specimens of *C. bowsheri* and *O. alleni* present in the bulk collections loaned from SINMNH and a subsample of 400 specimens of *C. cordata* selected randomly from a total of several thousand specimens.

Compared to *C. cordata, C. bowsheri* and *O. alleni* are relatively large. Only one of the 89 specimens of *O. alleni* was drilled and none of the 73 specimens of *C. bowsheri* were drilled (Fig. 3, Table 1). *C. cordata* ranges in size from 1.0 mm to 2.0 mm and 131 of 400

Table 1. Data summary

Species	No. of specimens	No. of specimens drilled	Largest specimen	Smallest specimen	Average size	Largest drilled specimen	Smallest drilled specimen	Average drilled specimen
C. bowsheri	73	0	8.8	4.2	6.9	N/A	N/A	N/A
O. alleni	89	1	5.8	2.9	4.2	3.8	3.8	3.8
C. cordata	400	131	2.0	1.0	1.5	2.0	1.0	1.5

specimens displayed drill holes (drilling intensity of 32.7%) (Table 1).

Drill holes in *C. cordata* are circular, perpendicular to the shell, and penetrate only one valve (Fig. 4). Note that, as stated above, all examined brachiopod specimens represent articulated shells with both valves preserved. The holes are small, ranging in size from 0.03 mm to 0.19 mm with a mean value of 0.1 mm. Many of the drill holes display slight beveling (see Fig. 4F) similar to that seen in drill holes made by naticid gastropods in the Cenozoic (Kabat 1990).

There were no occurrences of edge drilling and no repaired drill holes were observed. Also, there was no evidence of attachment scars on any of the analyzed specimens. Specimens that displayed two drill holes were not considered in quantitative analyses as this would require an arbitrary choice of which drill hole should be selected for analysis. Specimens with two drill holes are rare (only *c.* 5% of the specimens) and their exclusion does not affect the results in any notable manner.

Of the 131 drilled specimens of *C. cordata*, 124

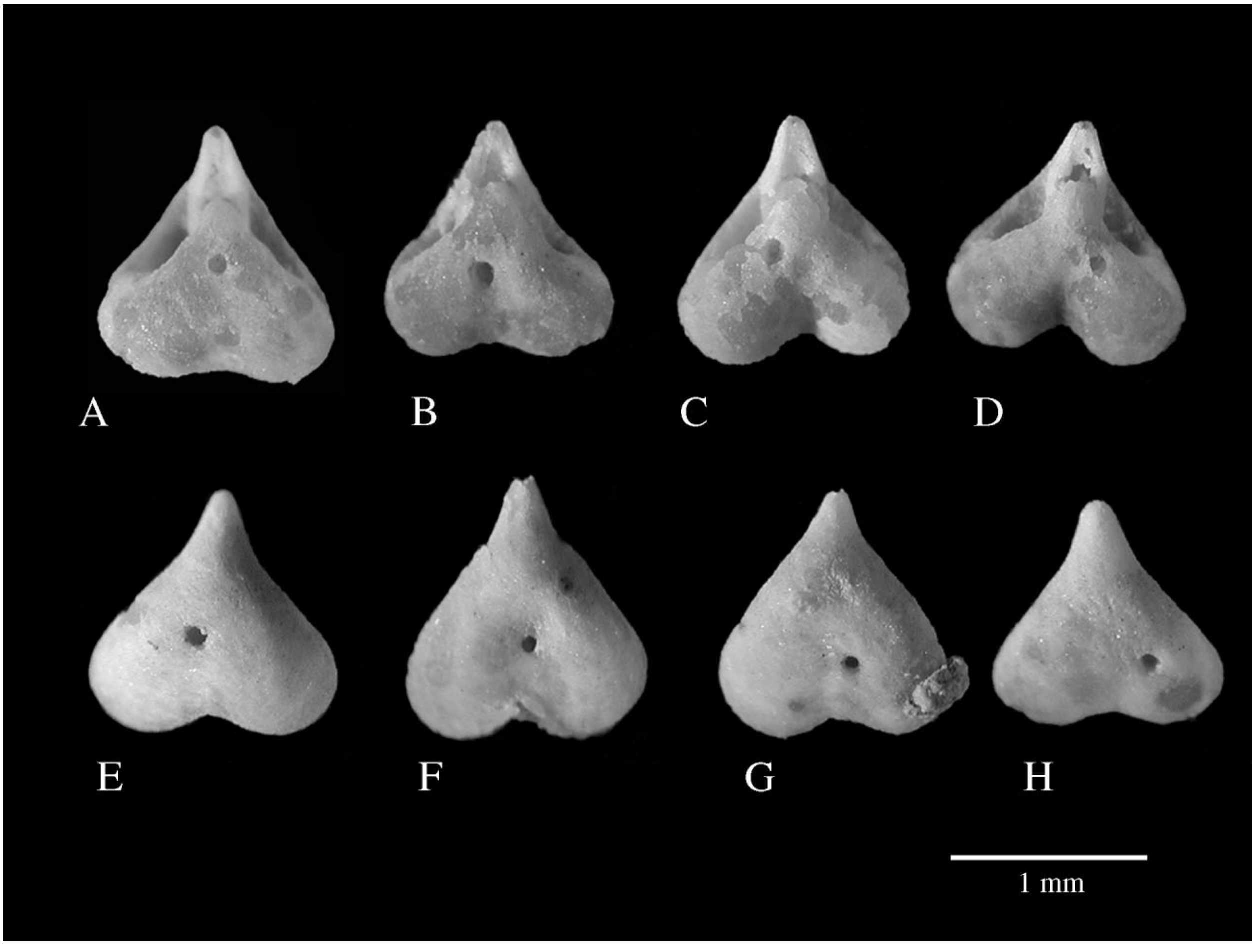

Fig. 4. Drilled specimens of *Cardiarina cordata*. A (USNM 519300), B (USNM 519301), C (USNM 519302), D (USNM 519303) display drill holes in dorsal valve. E (USNM 519304), F (USNM 519305), G (USNM 519306), H (USNM 519307) display drill holes in ventral valve.

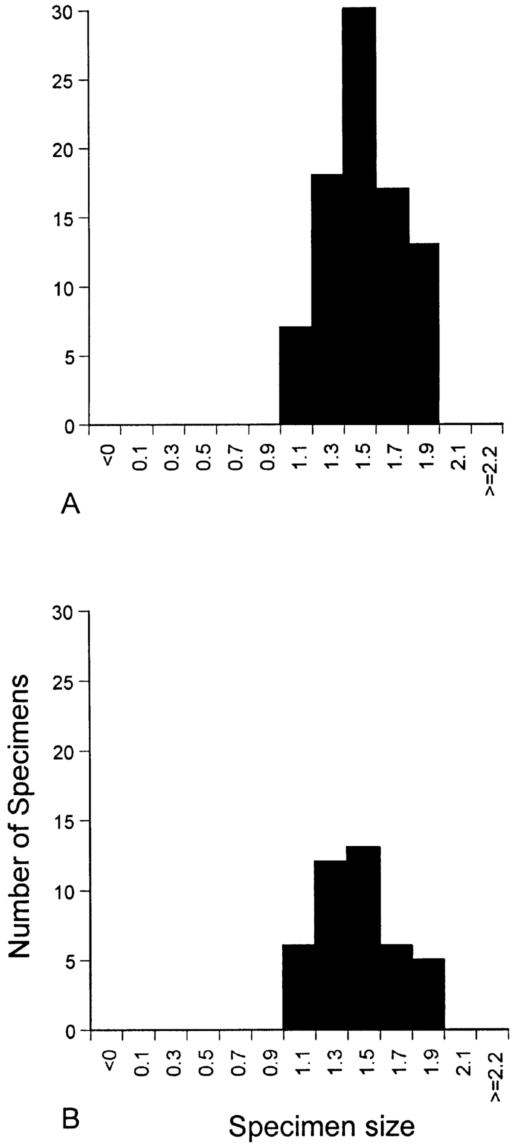

Fig. 5. Size frequency diagrams for specimens with a single drill hole. □A. Specimens with drill hole in the ventral valve. □B. Specimens with drill hole in the dorsal valve.

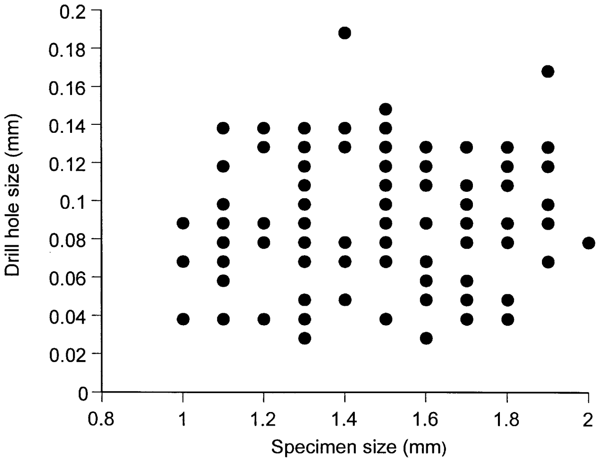

Fig. 6. Scatter plot of drill-hole size versus specimen size. Drill-hole size is maximum drill-hole diameter measured digitally from images. Specimen size measured as anterior-posterior length of the ventral (pedicle) valve. The plot includes all analyzed specimens of *Cardiarina cordata* that contained drill holes.

possess a single drill hole in either the ventral (pedicle) or dorsal (brachial) valve. Nearly two-thirds (81 of 124; 65.3%) of the specimens are drilled ventrally, whereas just over one-third are drilled dorsally (43 of 124; 34.7%). There is thus a pronounced and statistically significant preference for drilling in the ventral valve (Fisher exact test, $p \ll 0.05$). On the other hand, size frequency diagrams for specimens of *C. cordata* drilled dorsally and ventrally are statistically indistinguishable in their shape and median size (Fig. 5) (Wilcoxon test, $Z = -1.25$, $p = 0.22$; Kolmogorov-Smirnov test, $D = 0.13$, $p = 0.7$).

Seven specimens have two drill holes (5 of the 7 have both drill holes in the ventral valve (Fig. 4F) while two have a single drill hole in each valve). No specimens were observed with two drill holes in the dorsal valve. Neither of the two specimens that possess drill holes in both valves have the drill holes directly opposite each other, indicating that each drill hole was the result of an independent drilling event, and not a record of a single penetration that passed through both valves.

Specimen size was plotted against drill-hole size for all drilled specimens (Fig. 6). Spearman rank correlation shows that there is no significant positive correlation between the two variables ($r = 0.13$) and visual inspection of the plot does not suggest any, even weak, association between drill-hole diameter and specimen size.

There is definite selectivity in the site of the drill holes in *C. cordata*. As noted by Cooper (1956), drill holes in *C. cordata* occur in any part of the shell except the beak. This is also true for our data: most of the holes are located centrally, although a few are located along the shell margins. Visual inspection of drill-hole location in *C. cordata* specimens appears to show that drill holes in the ventral valve are more widely distributed than drill holes in the dorsal valve (Fig. 7A, B). However, Hotelling's T^2 test on the samples of shape (Bookstein) coordinates (see Dryden & Marda 1998) for dorsal versus ventral holes does not indicate any significant difference in the preferred position of holes ($F = 1.94$, $p = 0.15$) (note also that there are nearly twice as many holes drilled ventrally which may account for the wider range of hole location observed for ventral valves).

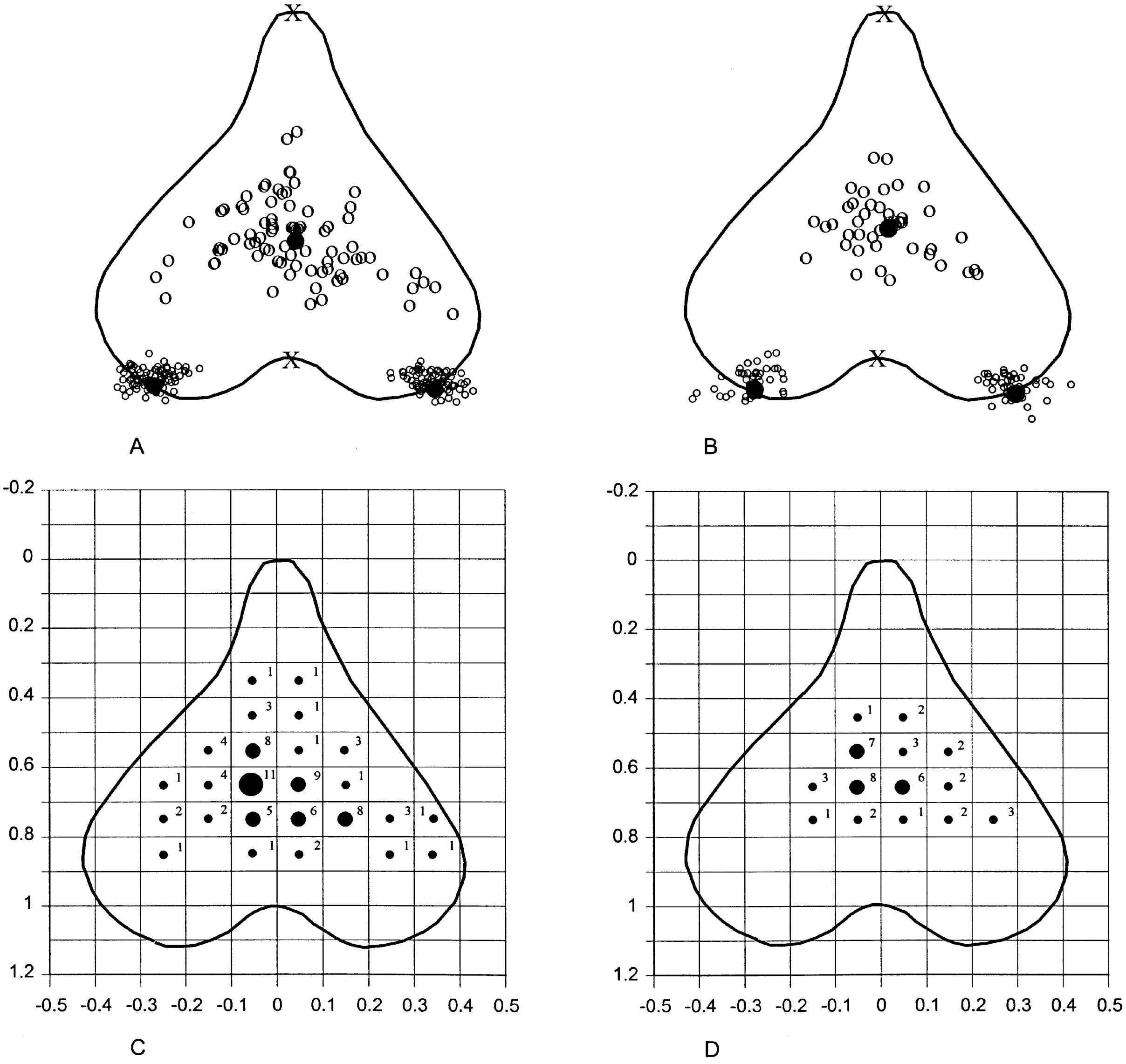

Fig. 7. □A, B. Plot of shape (Bookstein) coordinates of drill holes in ventral (A) and dorsal (B) valve. Endpoints of a standard reference baseline are indicated by X's. Type II landmarks for points of maximum curvature for each lobe are indicated by small open circles, drill holes are indicated by large open circles. Average values for points of maximum curvature and drill-hole location are indicated by filled circles. □C, D. Sector frequency distribution of drill holes with respect to a uniform grid for ventral (C) and dorsal (D) valve. Size of the circle indicates number of occurrences in each sector, 1 to 5 small circle, 5 to 10 medium circle, and more than 10 large circle. Number of occurrences are listed in an upper corner of each sector.

Using a uniform grid a sector-frequency distribution of drill holes in each valve was acquired (Fig. 7C, D). These distributions were compared against Poisson distributions to calculate expected χ^2- and G-values (see also Reyment 1971). Monte Carlo simulations with 10,000 iterations were run to determine if the observed values could be derived from a random Poisson-distributed population (see Kowalewski *et al.* 1997 for procedural details). The simulation produced highly significant results (ventral valve p (χ^2) = 0.0001, p (G) = 0.0001; dorsal valve p (χ^2) = 0.0002, p (G) = 0.0001), indicating that the drill holes are highly non-random in their location (Fig. 8).

Discussion

Paleoecological implications

The results indicate the presence of drilling organisms in the Pennsylvanian that showed highly selective behavior in choosing prey/host species and the site of

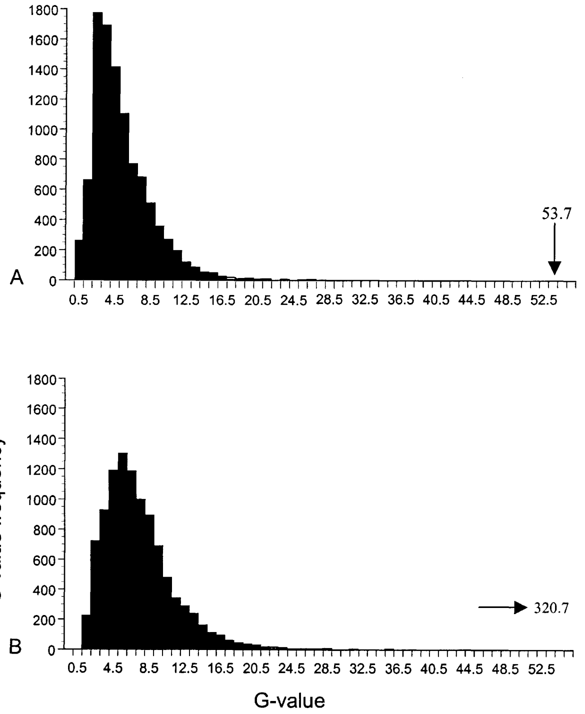

Fig. 8. Frequency distribution of G-values from Monte Carlo simulations of Poisson models for dorsal and ventral distribution of drill holes (10000 iterations each). ☐A. Ventral valve. ☐B. Dorsal valve. Arrows indicate the actual G-values computed from the distributions of drill holes as shown in Fig. 7C and D, respectively.

the attack. The exact identity of the driller is not known. Cooper (1956, p. 529) noted that '[m]any small gastropods occur in the siliceous residues with *Cardiarina* and one or more of them is probably responsible for the boring'. The suggestion that the borer was a gastropod is not unreasonable. Although no direct evidence for gastropod drilling can be presented here, Baumiller (1996) documented a platyceratid gastropod preserved on top of a drill hole in a blastoid providing thus a direct evidence that at least one group of Paleozoic gastropods was capable of drilling.

Drill holes observed in *C. cordata* are similar in size to Type A drill holes described by Ausich & Gurrola (1979; see also Smith *et al.* 1985; Leighton 2001); however, unlike Type A drill holes of Ausich & Gurrola (1979), these holes are beveled and the incidence of multiple complete holes is low. This is in contrast to relatively larger, but much less common, drill holes (Type B of Ausich & Gurrola 1979) documented for larger Paleozoic brachiopods, echinoderms, and mollusks. There are several differences between the drill holes reported here and those described by Ausich & Gurrola (1979). First, the drill holes observed here display beveled edges. Second, no incidence of repair to the drill hole was seen. Third, the incidence of multiple drill holes on a single specimen is low.

While the exact identity of the drilled cannot be established conclusively from drill-hole size and morphology or other data available here, the holes are clearly biologic in origin (i.e. they are not the result of taphonomic processes) and it is unlikely that they record post-mortem events (e.g. substrate borings). This is because the holes are typically singular, penetrate only one valve, vary in a narrow size range, and are regular (and generally invariant) in shape. Moreover, while substrate borers can generate holes in empty shells, they are unlikely to have produced simultaneously multiple stereotypic patterns observed here (i.e. species selectivity, size selectivity, site selectivity, and valve selectivity). Therefore, the holes, most likely record biotic interactions between living prey/host and their drillers.

The exact nature of the interaction recorded by drillers is more difficult to establish, especially without knowing the identity of the attacker. Unlike in the case of Type A drill holes reported by Ausich & Gurrola (1979) and interpreted by those authors as parasitic in origin, the small holes documented here may be of predatory origin (although parasitism cannot be entirely excluded). First, there is a nearly 100% success rate for all drilled specimens observed; that is, unfinished/incomplete holes and repaired holes are absent. Second, only a few specimens have more than one hole; similarly, marginal notes about drilled specimens scattered in the taxonomic literature on cardiarinids do not include any mention of multiple drill holes (see also below). Third, no attachment scars were observed, although the process of silicification may have altered or destroyed any evidence of scarring. Finally, the drill holes (see Fig. 7) are generally located in an area that could offer access to the soft tissue of the animal (see also below). These lines of evidence are suggestive of predation, but parasitism cannot be ruled out here entirely.

In sum, regardless of whether the drillings represent predatory or parasitic activity, the intent of the attack was clearly detrimental (perhaps lethal) to the prey/host. It is thus particularly noteworthy that the drilling intensity observed here (32.7%) is among the highest reported for any Paleozoic brachiopod taxon and is comparable to Cenozoic levels of predation (Kelley & Hansen 1993; Kowalewski *et al.* 1998; Hoffmeister & Kowalewski 2001). This suggests that predatory/parasitic pressure on Paleozoic benthic taxa was locally high even though the overall pattern is one of low intensity. However, the relationship between drilling intensity (as indicated by the percentage of individuals

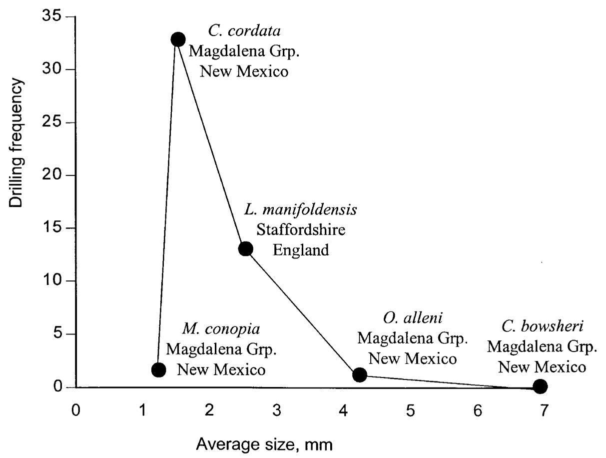

Fig. 9. Comparison of drilling frequency for the four described species from the Magdalena Formation and the Mississippian cardiarinid *L. manifoldensis* from England. Average size corresponds to data from Table 1 for *C. codata, O. alleni,* and *C. bowsheri*. Average size for *M. conopia* is from Grant (1988), average size for *L. manifoldensis* is from Brunton & Champion (1974).

drilled) and actual intensity of biotic interactions is ambiguous (see especially Leighton 2002; Kowalewski 2002). There is a growing body of evidence suggesting that encounter rate is the important factor in predation intensity; with potential victims that live in dense patches showing a higher frequency of attack than potential victims that are scattered. Also, predators/parasites may be facultative borers, so drilling frequencies may severely underestimate the actual levels of interactions. Nevertheless, high drilling frequencies recorded here clearly show that, occasionally, high (Cenozoic-like) levels of predation/parasitism affected Pennsylvanian cardiarinid prey/host.

Stereotypy patterns

The strong stereotypy patterns displayed by drillers in terms of (1) species and/or size selectivity, (2) valve selectivity, and (3) site selectivity are remarkable, especially considering limited behavioral information available in the literature for Paleozoic drillers. These patterns are therefore discussed here in more detail.

There appears to have been a very strong selectivity by the driller for a single species of small brachiopod from the Magdalena Group. While two of the three described species are drilled, only *C. cordata* is drilled intensely. The prey/host species selection may be controlled by specimen size. The smallest species described by Cooper (1956) has the highest drilling intensity while the larger species have lower drilling intensities (Table 1). If this is the case, the critical size threshold for the predator/parasite is very narrow. Grant (1988) described a second cardiarinid brachiopod, *Minysphenia conopia*, from the same residues that produced *C. cordata, O. alleni,* and *C. bowsheri.* This species is smaller than *C. cordata* (average size *c.* 1 mm) and is drilled, but at a much lower intensity (3 out of 200 or 1.5%; Grant 1988, p. 125). *O. alleni* has an average anterior-posterior length of 4.2 mm and has similar drilling intensity to *M. conopia*. If specimen size is the determining factor for the predator/parasite, then it is logical to expect that juveniles of many larger species would also be subject to predation when they fall into the proper size range. Since all specimens of the three species described by Cooper (1956) were examined, any juveniles of *C. bowsheri* and *O. alleni* are included in the data presented here. There is no overlap in the size range of *C. bowsheri* and *O. alleni* with *C. cordata*, although the one drilled *O. alleni* specimen is on the smaller end of the size range for the species (Fig. 3). Cooper (1956) does mention that juveniles of several larger brachiopods were also recovered from the residues but provides no information on drilling in those specimens.

A similar pattern of apparent size selectivity is seen in the taxonomic literature for the Family Cardiarinidae. Nine species have been described to date; six were reported as having drill holes. These species are *C. cordata, Lambdarina manifoldensis* Brunton & Champion, 1974, *Minysphenia conopia* Grant, 1988, *L. glaphyra* Bassett & Bryant, 1993, *L. brownendensis* Morris, 1994 and *Hampsia cooperi* Morris, 1994. *L. granti* Nazer, 1983 is not reported as being drilled, but one of the figured specimens (Nazer 1983, fig. 1C) appears to have a drill hole. All reported drill holes are similar in size and shape to those seen in *C. cordata*. Drill-hole location generally is not restricted to one part of the shell, but Brunton & Champion (1974) report most of the drill holes on *L. manifoldensis* to be near the midline of the shell. *Lambdarina manifoldensis*, the only other cardiarinid species for which quantitative drilling data are available, is larger than *C. cordata*. While rigorous size data are not available for *L. manifoldensis*, Brunton & Champion (1974, p. 820) state that the maximum length for this species is 2.5 mm. Morris (1994) provides measurements of four specimens of *L. brownendensis* (average anterior-posterior length of 2.5 mm) and states that *L. brownendensis* is of comparable size to *L. manifoldensis*. Again, in this slightly larger species a lower drilling intensity is observed (7 out of 54 specimens or 12.9%; Brunton & Champion 1974) than that seen in *C. cordata* (Fig. 9). Of additional interest are drilled juvenile forms of two species, *L. brownendensis* and *L. glaphyra* (Morris 1994; Bassett & Bryant 1993). It is worth noting that the highest drilling frequencies ever reported for Paleozoic brachiopods are confined to small taxa (Leighton 2001; this study). These high drilling frequencies may be associated with Paleozoic predators/parasites that drill small holes and attack small prey/host species.

The preference for drilling the ventral valve is striking. Ventral valves are drilled with almost twice the frequency in *C. cordata*. This preference is also seen in other cardiarinid brachiopods. Brunton & Champion (1974) report that only 1 of the 7 drill holes (14.3%) in *L. manifoldensis* was in the dorsal valve. Although the number of specimens is much fewer, this is comparable to the preference seen in *C. cordata*, where about one-third of the drill holes are seen in the dorsal valve. Paleoecologic information for cardiarinid brachiopods is limited. Brunton & Champion (1974) suggested that *L. manifoldensis* lived in clusters attached either to a hard substrate or to other plants or animals, but Grant (1988) presented evidence from living brachiopods which showed that living on a soft substrate cannot be dismissed for these small brachiopods. All species in the Family Cardiarinidae appear to have had a functional pedicle, which suggests that none of the species lived infaunally. Given the uncertain ecology of cardiarinid brachiopods and the unknown identity of the driller, the observed valve preference is hard to interpret. While this preference may simply be due to the larger size of the ventral valve as a platform to drill in, it may also reflect behavioral aspects of the predators/parasites or prey/host.

Finally, there is also remarkable stereotypy in the site of drill holes in *C. cordata*. Although drill holes can occur anywhere on the shell except the beak, most of the holes are located near the midline of the shell on both valves. A similar pattern was noticed by Brunton & Champion (1974) for *L. manifoldensis* but no quantitative analyses were done for that species. There are compelling reasons for placing a drill hole in the mid-section of the valve, whether the intent of the attack is lethal predation or parasitism. Placing a drill hole near the center of the valve could provide access to the muscle field of any brachiopod, especially if the predator has some form of mobile proboscis, as well as to the limited amount of other soft tissue of the victim. If, on the other hand, the intent of the attack was parasitic in nature, a hole over the lophophore could provide access to the feeding current, although a drill hole located near the edge of the valve could also provide access to the inhalant current.

Summary

Specimens of *Cardiarina cordata* from the Pennsylvanian of New Mexico display evidence of intense drilling of either predatory or parasitic origin. The drill holes show high levels of stereotypy in location, both with respect to valve selection and drill-hole location on the valve. There is also extreme selection for prey/host species but this selectivity may be size related: species that are slightly larger or slightly smaller than *C. cordata* are attacked far less frequently. These results are similar to those of Leighton (2001) and suggest that two types of drillers may have existed in the Late Paleozoic with small prey/host species experiencing high frequencies of predation/parasitism and larger species experiencing low frequencies of attacks.

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