Shell ornamentation as a likely exaptation: evidence from predatory drilling on Cenozoic bivalves

Adiël A. Klompmaker and Patricia H. Kelley

Abstract.—Predation is an important process in modern oceans and in the evolutionary history of marine ecosystems. Consequently, it has been hypothesized that shelled prey modified their ornamentation in response to predation. However, bivalve ornamentation has also been argued to be important in maintaining a stable life position in the sediment and in burrowing. To test whether concentric ribs were effective against drilling by carnivorous gastropods, we examined drill hole position and completeness for four Cenozoic bivalve species that differ in rib strength (*Astarte radiata*, *A. goldfussi*, *Lirophora glyptocyma*, and *L. latilirata*). The percentage of drill holes located between the ribs increases with increasing rib strength, whereas the percentage of drill holes on top of ribs decreases. This result suggests that gastropods select the drill hole site more effectively as rib strength increases, thereby saving time and energy, and that natural selection favors gastropods that select drill hole sites between ribs. Because of this greater stereotypy, the percentage of drill holes that are incomplete is generally lower in strongly ribbed species. The proportion of drill holes located on top of ribs is greater for incomplete than complete holes, implying that ribs can be effective against predators, but only when selected as the drilling location. We show that ribs are most effective against drilling predation for bivalves with moderately sized ribs, between which gastropods have difficulty siting drill holes. Concentric ribs are unlikely to have evolved as an adaptation against drilling predation because concentric ribs evolved in the Paleozoic and were already common in the Mesozoic, whereas drilling frequency increased later, in the Late Cretaceous–Paleogene. Moreover, rib strength of North American *Astarte* did not change through this time interval. Thus, the ribs considered here are a likely exaptation to drilling given their effectiveness at deterring drilling predation on bivalves with moderate ribs.

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Introduction

The function and functional morphology of shells have been a topic of debate for many decades. Shells are thought to have evolved early in the history of biomineralizing metazoans during the Ediacaran and Cambrian to protect soft tissue ("the Verdun Syndrome" [Dzik 2005, 2007]). Among the phyla that developed a shell during that period were molluscs (e.g., Pojeta 1987; Dzik 2005), including Cambrian bivalves (e.g., Runnegar and Pojeta 1992; Elicki and Gürsu 2009; Zong-Jie and Sánchez 2012). Whereas the shell as a whole may be primarily for protection of the soft tissue inside the bivalve shell, ornamentation on the shell may serve a variety of purposes. Bivalve ornamentation has been postulated to be important for a variety of functions including maintaining a stable life position in the sediment, burrowing, shell strengthening, directing inhalant and exhalant currents, and protecting against predators (e.g., Trueman et al. 1966; Carter 1967, 1968; Kauffman 1969; Stanley 1970, 1981, 1988; Aller 1974; Thomas 1975; Arua and Hoque 1987; Harper and Skelton 1993; Kelley and Hansen 1996; Stone 1998; Harper and Kelley 2012). An anti-predatory function of ornamentation has also been suggested for Paleozoic and Mesozoic brachiopods (Leighton 2001, 2003; Vörös 2010; Johnsen et al. 2013), Cretaceous and Paleogene ostracods (Reyment 1967; Reyment et al. 1987), Jurassic nautiloids and ammonoids (Bardhan and Halder 2000; Kröger 2002), modern barnacles (Palmer 1982), and modern and fossil marine and continental

gastropods (e.g., Bertness and Cunningham 1981; Arua and Hoque 1987; Donovan et al. 1999; Paul et al. 2013; Liew and Schilthuizen 2014), although Yochelson et al. (1983) suggested that predation intensity on the sub-Holocene scaphopod *Dentalium laqueatum* increased with more ribs.

Various types of bivalve ornamentation have been proposed to serve an anti-predatory function, although Leonard-Pingel and Jackson (2013) suggested ornamentation was not effective against drilling predation in a study that lumped all types of ornamentation and used a variety of bivalves. Spines have been argued to prevent predation (Carter 1967; Stone 1998); spines may promote epibiont settling, thus camouflaging epifaunal bivalves from predators (Feifarek 1987; Carlson Jones 2003; Mackensen et al. 2012; but see Willman 2007). An increase in the strength of radial ribs in Cretaceous exogyrine bivalves was linked to durophagous predation (Dietl et al. 2000). The latter was supported by Alexander and Dietl (2003), who argued that radial ribs are more common in modern tropical bivalves experiencing a higher intensity of predation than in bivalves in more temperate waters. Concentric ornamentation has received relatively little study with regard to drilling predation, with some indications that concentric ribs may affect drilling behavior in that drill holes tend to be located between smooth-topped concentric ribs (Arua and Hoque 1989; Klompmaker 2011) or concentric lamellae (Ansell and Morton 1985; Anderson et al. 1991). Drill holes between this type of ornament have also been figured in the literature for ribs (e.g., Hayasaka 1933: Pl. 1; Simões et al. 2007: Fig. 5B,C; Ottens et al. 2012: Fig. 2C) and lamellae (e.g., Robba and Ostinelli 1975: Pl. 43.1; Hingston 1985: Fig. 6A; Roopnarine and Beussink 1999: Fig. 1). These observations may suggest that ribs and lamellae are ineffective against this type of predation. However, the strength of concentric ornament varies greatly among bivalves and the effectiveness of drill holes on ribs is largely unknown. Thus, it is premature to suggest that concentric ornament fails to serve as a protection against drilling predators such as muricid and naticid gastropods, which are important predators of bivalves in modern and ancient oceans (e.g.,

Kabat 1990; Kowalewski 1993; Kelley and Hansen 2003; Dietl et al. 2004; Klompmaker 2009; Sawyer and Zuschin 2010; Chattopadhyay et al. 2013).

We here address the degree to which ornamentation is effective against drilling predation by studying several bivalve species with varying strengths of smooth-topped concentric ribs. We investigate (1) the percentage of incomplete drill holes per species, (2) the stereotypy of drill hole site location per species, (3) the drilling frequency of two congeneric species with different ornamentation from the same locality, (4) the proportion of incomplete drill holes on ribs versus between ribs, and (5) drill hole size on ribs versus between ribs. Our results show that concentric ribs do influence the drilling behavior and success of gastropods. We also assess whether this type of shell ornamentation serves as an adaptation or exaptation to drilling predation (see discussion in Harper 2006 and Harper and Kelley 2012). The definitions of adaptation and exaptation used herein follow Gould and Vrba (1982): adaptations are features built by natural selection for their current role, whereas exaptation refers to characters that evolved for other usages or for no particular function and were co-opted later for their current role.

Materials and Methods

To test the effectiveness against drilling predation of smooth-topped concentric ribs that are symmetrical in cross-section, we examined gastropod drill hole size, position, and completeness for four Cenozoic bivalve species (Fig. 1). All display ribs that are approximately equal in width to the spaces (valleys) between them, but they differ in coarseness of ribs (*Astarte radiata*, *A. goldfussi*, *Lirophora glyptocyma*, and *L. latilirata*, ordered by increasing rib strength). All four species are relatively sedentary because of their concentric ribs (Stanley 1970), so morphology rather than mobility should be of prime importance in defense. Specimens of *Astarte* were collected at the Miste locality near Winterswijk, Gelderland province, the eastern Netherlands (Janssen 1984), from middle Miocene ("Hemmoorian") sediments assigned to the Miste Bed, Aalten Member, Breda Formation (Van den Bosch
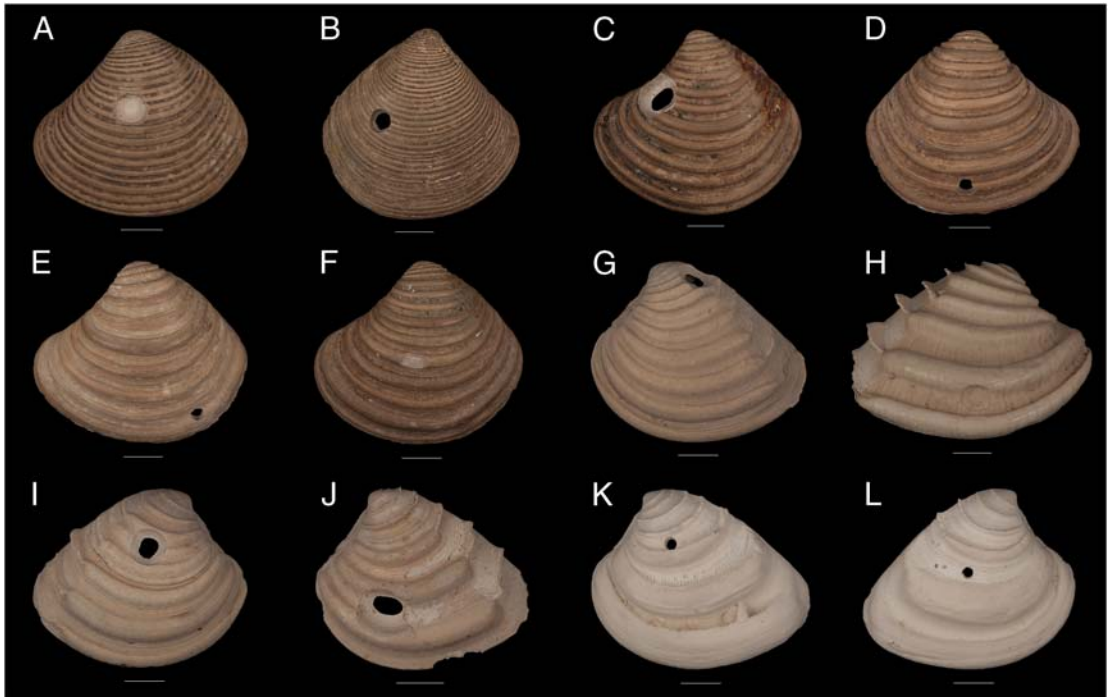
FIGURE 1. Specimens of the four studied Cenozoic bivalve species showing complete and incomplete drill holes. A, B. *Astarte radiata* from the Miocene of Miste, Breda Formation, The Netherlands (RGM.794165K–794165L). C–F, *Astarte goldfussi* from the Miocene of Miste, Breda Formation, The Netherlands (RGM.607538K–607538N). G–J, *Lirophora glyptocyma* from the Miocene of Oak Grove, Oak Grove Sand, Florida (UF 244747–244750). K–L, *Lirophora latilirata* from the Pliocene of the Acline Borrow Pits 01, Tamiami Formation, Florida (UF 244751–244752). Scale bars, 2.0 mm.

et al. 1975). More specifically, specimens of *A. goldfussi* and *A. radiata* were collected from the *Hiatella arctica* acme zone or the base of the *A. radiata* acme zone within the Miste Bed. Specimens of *L. glyptocyma* were collected in the lower Miocene Alum Bluff Group (Oak Grove Sand) at the Oak Grove locality, Okaloosa County, Florida, U.S.A.; specimens of *L. latilirata* were collected from the Pliocene Tamiami Formation (Pinecrest beds) at the Acline Borrow Pits 01 locality, Charlotte County, Florida, U.S.A.

Antero-posterior shell length was measured using calipers accurate to ≤0.03 mm. Because drilling parameters may vary with prey size (Ottens et al. 2012), interspecific comparisons of drilling parameters were conducted at a standardized shell length. A length of 5.1–10.0 mm was selected for data standardization because of the abundance of specimens of this range in these faunas.

Rib characteristics were compared for ten undrilled specimens in the length range of 9.1–10.0 mm for each species. The number of concentric ribs was tallied and total shell thickness (including the rib) was measured at the second rib from the commissure. Shell thickness between ribs was measured midway between the anterior and posterior margin in the valley dorsal or ventral to the second rib from the commissure, depending on which was more accessible. Rib thickness of each specimen was calculated by subtracting the shell thickness between the ribs from the total shell thickness. Rib spacing was determined by measuring the distance from the top of the rib to the next rib around rib 2 or 3 from the commissure. Shell thickness between ribs, rib thickness, the number of ribs per species, and rib spacing were compared using the nonparametric Kruskal-Wallis test instead of ANOVA, because not all data followed a normal distribution. The null hypothesis is that the samples are taken from populations with equal medians for the three parameters tested. The subsequent Bonferroni corrected Mann-Whitney pairwise comparisons tests were used in PAST. For all tests, alpha is 0.05.

Drill holes were categorized as complete (penetrating to the interior of the valve) or incomplete; incomplete drill holes generally indicate failed predation attempts (Kelley and Hansen 2003; Visaggi et al. 2013). The percentage of drill holes that were incomplete (termed prey effectiveness, PE, by Vermeij [1987]) was determined for each species. Drilling frequencies (DF) at the standardized size were determined only for the two species of *Astarte*, both from the same locality and stratigraphic age, by dividing the number of completely drilled valves by one-half the total number of valves, to account for the fact that each *Astarte* individual consists of two valves. We compared drilling frequencies for these two species by using a Pearson's chi squared test. DFs were not calculated for the two other species because samples differed in age and/or locality, implying that comparing those values is not meaningful because differences in DF would not be attributable solely to rib strength.

The location of the center of each complete or incomplete drill hole was categorized as "between ribs," "on rib," or "other" for drilled specimens of each species. The latter category refers to those holes that were centered on the boundary between a valley and rib, those that were too large relative to the ribs to determine the location of the center (see Fig. 1A), or those situated on the lunule or escutcheon. Six pairwise Fisher's exact tests compared the number of occurrences in the three drill hole categories for each of the four species, based on the null hypothesis that proportions of drill holes are equal for the three drill hole locations. A Bonferroni corrected alpha of 0.0083 (instead of 0.05) was used.

For the subset of drill holes small enough to fit completely between adjacent ribs, the category "between ribs," "on rib," or "middle" was assigned for each drill hole; those that were placed on the lunule or escutcheon were excluded from this analysis. "Middle" refers to drill holes that are located partly in the valley and partly on the rib. This analysis was not possible for *Astarte radiata* because of the close spacing of ribs. For *A. goldfussi* we used additional specimens from the same collection, horizon, and locality to increase sample size of drill holes that fit between ribs; no additional specimens were available for *L. glyptocyma*. A Fisher's exact test was performed to compare *A. goldfussi* and *L. latilirata* given their sufficient sample size (~30 specimens each).

We tested the effect of ribs on the completeness of drill holes for several coarse-ribbed species as described below. Samples with at least 30 drilled specimens with holes of any size relative to ribs that were centered either on or between the ribs were studied for this purpose. Positions of incomplete and complete drill holes were compared for *A. goldfussi* and *L. glyptocyma* (length 5.1–10.0 mm). In order to increase the number of samples, we also conducted comparisons for several additional samples of *Lirophora* spp., using all drilled specimens regardless of length: *L. athleta* from the Jackson Bluff locality, Jackson Bluff Formation (*Cancellaria* zone), upper Pliocene, Florida, U.S.A.; *L. athleta* from the Richardson Road Shell Pit locality, Tamiami Formation (Pinecrest beds), Pliocene, Florida, U.S.A.; *L. glyptocyma* (locality and age as above); *L. latilirata* from the Register Quarry near Old Dock (lower Waccamaw Formation), lower Pleistocene, North Carolina, U.S.A. Pairwise Fisher's exact tests were conducted on the number (and percentage) of incomplete and complete drill holes for drill holes on ribs and between ribs using an alpha of 0.05. The null hypothesis is that the percentage of incomplete drill holes on ribs is equal to that between ribs.

To investigate whether complete and incomplete drill holes differed in size, we measured with calipers the outer drill hole diameters of drilled specimens of *A. goldfussi* and *A. radiata* (The Netherlands) and *L. glyptocyma* and *L. latilirata* from Florida (all in the length range of 5.1–10.0 mm) and of all sizes of *L. latilirata* from the Register Quarry in North Carolina. Where permitted by sample size (restricted to at least 30 drilled specimens, at least ten of which exhibited an incomplete drill hole), results were analyzed separately for holes of any size relative to the ribs, holes larger than the valley between ribs, and holes that fit between the ribs. We used Mann-Whitney *U*-tests with alpha of 0.05 to test the null hypothesis that the sizes of incomplete and complete drill holes do not differ within a sample.

To test whether the rib strength of *Astarte* spp. changed during the time interval in which drilling became more abundant (Late Cretaceous–Paleocene [see Kowalewski et al. 1998; Huntley and Kowalewski 2007]), figured occurrences of Jurassic–Paleogene *Astarte* from North America were classified from 1 (weak ribs) to 5 (strong ribs) at the period-level and the mean was calculated for each period. We used a Kruskal-Wallis test to investigate the hypothesis that the medians are equal using an alpha of 0.05. For data on occurrences and references to articles containing the figures we consulted the Paleobiology Database (2014): Jurassic (Cragin and Stanton 1905; Jaworski 1929; Fürsich 1982; Poulton 1991; Vega and Lawton 2011); Cretaceous (Imlay 1940; Stoyanow 1949; Cserna 1956; Richards et al. 1958; Perrilliat et al. 2000); Paleogene (Dockery 1982; Rossbach and Carter 1991). North American occurrences of *Astarte* for this time interval were common and figured frequently, relative to those from north-western Europe. The same method could not be used for *Lirophora* because its earliest occurrence is Cenozoic in age (Paleobiology Database 2014).

Specimens exhibiting more than one drill hole, which was rare, were excluded from all analyses in all methods used in this research. All statistical analyses were performed in PAST 2.17 (Hammer et al. 2001).

Institutional abbreviations: UF – University of Florida, Florida Museum of Natural History (Invertebrate Paleontology), Gainesville, Florida.; RGM – Naturalis Biodiversity Center, Leiden, The Netherlands.

Results

Shell Characteristics.—Kruskal-Wallis tests comparing shell thickness between the ribs, rib thickness, total shell thickness, and the number of ribs all returned p-values < 0.05, suggesting that the medians differ among species. Results of the subsequent Mann-Whitney tests are as follows: *Astarte radiata*, *Lirophora glyptocyma*, and *L. latilirata* have a statistically indistinguishable shell thickness between the ribs for the length range of 9.1–10.0 mm, whereas this thickness is less for *A. goldfussi* than for *Lirophora* spp. (Table 1, Fig. 2A). Rib thickness, and consequently total

TABLE 1. *p*-values using the Mann-Whitney pairwise comparison test for four shell characteristics.

Shell characteristic	*A. radiata*	*A. goldfussi*	*L. glyptocyma*
Shell thickness in valleys			
Astarte radiata			
A. goldfussi	0.054		
Lirophora glyptocyma	1.000	0.034	
L. latilirata	1.000	0.013	1.000
Rib thickness			
A. radiata			
A. goldfussi	0.001		
L. glyptocyma	0.001	0.039	
L. latilirata	0.001	0.001	0.006
Rib + shell thickness in valleys			
A. radiata			
A. goldfussi	0.082		
L. glyptocyma	0.001	0.001	
L. latilirata	0.001	0.001	0.093
Number of ribs			
A. radiata			
A. goldfussi	0.001		
L. glyptocyma	0.001	0.001	
L. latilirata	0.001	0.001	0.001
Rib spacing			
A. radiata			
A. goldfussi	0.001		
L. glyptocyma	0.001	0.002	
L. latilirata	0.001	0.001	0.001

shell thickness, significantly increases from *A. radiata* to *L. latilirata*; nearly all pairwise comparisons between species are statistically significant. Conversely, the number of ribs decreases from *A. radiata* to *L. latilirata* (Table 1, Fig. 2B). Rib spacing increases significantly from *A. radiata* to *L. latilirata* (Table 1, Fig. 2C). As the thickness of ribs increases so does rib width and spacing, leaving space for fewer ribs, which results in an inverse relationship of rib thickness and number of ribs.

Incomplete Drill Holes, Drilling Frequency, and Placement of Drill Holes.—The percentage of drill holes that are incomplete (i.e., prey effectiveness) is <10% for all species when data are size standardized. Strongly ribbed species of *Lirophora* have PE values <4% (Fig. 3). Although the prey effectiveness in the stronger-ribbed *Astarte goldfussi* appears higher than that of *A. radiata* (10.3 vs. 8.7%), the difference is not statistically significant ($\chi^2 = 0.23$, $p = 0.8911$). Drilling frequency for *A. radiata* within the length range 5.1–10.0 mm is 0.343 (181 drilled valves of a total of 1055). In contrast, the stronger-ribbed shells of
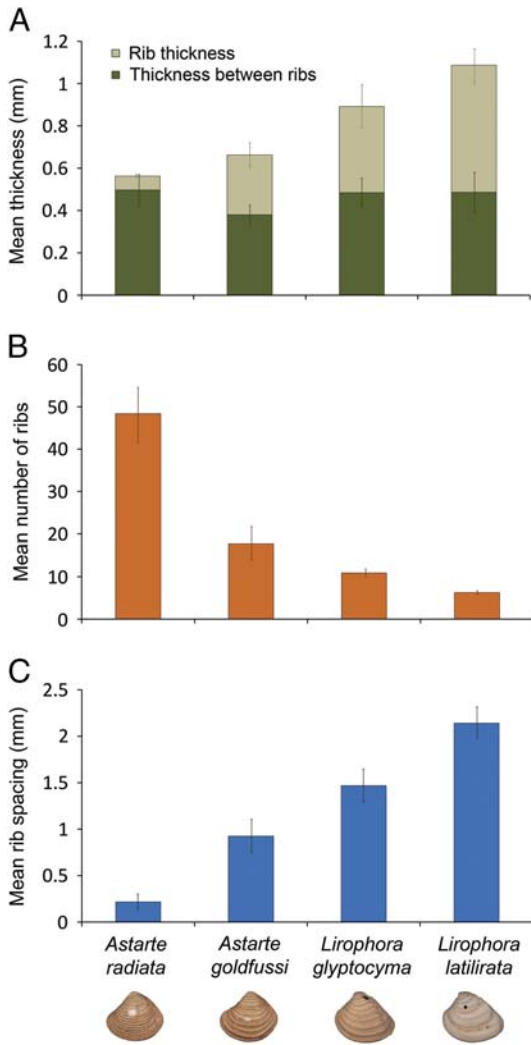
FIGURE 2. Rib thickness, number, and spacing based on ten specimens for each of the four species within the length range 9.1–10.0 mm. A, Total mean thickness of the shell consisting of the thickness of the rib and the shell thickness between the ribs. B, Mean number of ribs. C, Mean rib spacing. Error bars are ± 1 SD.

FIGURE 3. Percentage of drill holes that are incomplete for the four species, based on drilled specimens in the length range 5.1–10.0 mm.

A. goldfussi have a significantly lower DF of 0.271 (183 / 1353) ($\chi^2 = 6.09$, $p = 0.013$).

The position of drill holes relative to ribs could not be determined for *A. radiata* because of the small size of the ribs relative to the drill holes. Our results for all other species indicate that the percentage of drill holes for which the center is located between the ribs increases with rib strength for drill holes of any size, from 10% (*A. goldfussi*) to 84% (*L. latilirata*). In contrast, the percentage of drill holes with the center on top of ribs decreases with increasing
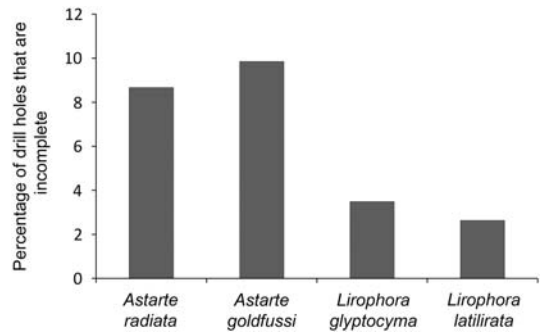
rib strength from *A. goldfussi* (40%) to *L. latilirata* (3%) (Table 2, Fig. 4A). Six pairwise Fisher's exact tests on the number of occurrences in the three drill hole categories of the four species all returned *p*-values < 0.0083 (= Bonferroni corrected alpha using 0.05), indicating that the drill holes are placed differently for every pair of species. The percentage of drill holes classified as "other" is lower in more strongly ribbed species. When only drill holes that could fit between the adjacent ribs are taken into account, *A. goldfussi* has a higher percentage of holes on ribs and a lower percentage of holes between ribs than *L. latilirata* (Table 2, Fig. 4B); the difference in drill hole placement is statistically significant (Fisher's exact test: *p* <0.05).

As shown by the results of the Fisher's exact tests, significantly more incomplete holes of any size occur on ribs than between ribs for half of the tests. Results appear influenced by the relatively low number of specimens, as two of the non-significant results are significant when Fisher's exacts tests were performed on percentages instead of numbers (Table 3). In the latter case, all samples except *Lirophora glyptocyma* with a length range of 5.1–10.0 mm returned significant differences (Fig. 5).

Drill Hole Size and Ribs.—Statistical comparisons of the drill hole diameter of complete and incomplete holes could be carried out only for the North Carolina samples of *Lirophora latilirata* and the two species of *Astarte*. We could not use Florida samples of *L. latilirata* or *L. glyptocyma* because the minimum number of incomplete drill holes was not reached, as was the case for drill holes

TABLE 2. Location of drill holes in specimens of four species.

	Drill hole of any size relative to ribs			If drill hole fits between ribs		
	Center on rib	Center between ribs	Other	On rib	Between ribs	Middle
Astarte radiata	0	0	150	0	0	0
A. goldfussi	81	21	101	14	8	10
Lirophora glyptocyma	9	30	47	0	3	0
L. latilirata	1	32	5	1	26	1

that could fit between the ribs for both species of *Astarte* and *L. latilirata* (NC). For categories with sufficient numbers of drilled specimens, our results indicate that all mean drill hole sizes for incomplete drill holes are smaller than those for complete drill holes. The results are significant for both species of *Astarte* but not for *L. latilirata* (Table 4, Fig. 6), including when the size range is restricted to 25.1–30.0 mm. Data on sizes of drill holes present in each species can be found in the Supplementary Table.

Rib Strength in Astarte.—Despite a limited sample size, rib strength of North American *Astarte* remained relatively stable through the studied time interval: Jurassic (2.4, 7 occurrences), Cretaceous (2.5, 6 occurrences), and Paleogene (2.5, 4 occurrences). The Kruskal-Wallis test returned a *p*-value of 1, suggesting that the medians are not statistically different. Because rib strength and rib spacing are positively correlated ($r^2 = 0.997$; $p = 0.001$) based on data underlying Figures 2A and 2C, we can conclude that rib spacing also did not change.

Discussion

Identity of the Predator.—The (subcircular) outline of the drill holes, three-dimensional shape, size, and orientation perpendicular to the shell surface all point to drill holes produced by gastropods. The beveled shape of most drill holes (e.g., Fig. 1) suggests predation by naticid gastropods, though muricid drillers likely produced some of the holes studied here. Specimens of both Muricidae and Naticidae are common in all stratigraphic levels studied (Janssen 1984; Florida Museum of Natural History Invertebrate Paleontology Online Database 2013).

Comparing Species from Multiple Localities and Stratigraphic Levels.—This study uses material from multiple locations and stratigraphic levels because we are unaware of an assemblage of related species from the same locality and age displaying such a broad range in rib morphology as studied herein. This approach raises the
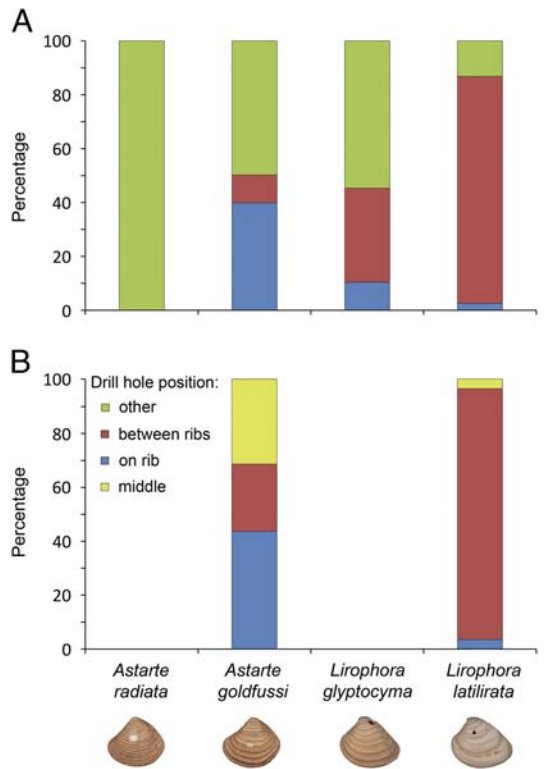

FIGURE 4. Location of drill holes relative to the ribs of bivalve species with increasing rib strength (left to right) for specimens with length of 5.1–10.0 mm. A, The proportion of drill holes with the center located between the ribs increases, whereas the proportion of drill holes on ribs decreases, as rib strength increases. Specimen count: *Astarte radiata* = 150; *A. goldfussi* = 202; *Lirophora glyptocyma* = 86; *L. latilirata* = 38. B, The proportion of holes fitting entirely between the ribs is markedly higher for *L. latilirata* than for *A. goldfussi*. A bar could not be shown for *A. radiata* because none of the drill holes fit between the ribs; sample size for *Lirophora glyptocyma* was only 3. Specimen count: *A. goldfussi* = 32; *L. latilirata* = 28. "Other" refers to those holes that were centered on the boundary between a valley and rib, those that were too large relative to the ribs to determine the location of the center (see Fig. 1A), or those situated on the lunule or escutcheon. "Middle" refers to drill holes that are located partly in the valley and partly on the rib.

TABLE 3. Results of Fisher's exact tests comparing the occurrence of complete vs. incomplete drill holes on ribs and between ribs for numbers and percentages.

	Numbers (p-value)	Percentages (p-value)
Lirophora athleta (Jackson Bluff Formation)	<0.001	<0.001
L. athleta (Tamiami Formation)	0.166	0.006
L. glyptocyma (Alum Bluff Group)	<0.001	<0.001
L. latilirata (Waccamaw Formation)	<0.001	<0.001
Astarte goldfussi (Breda Formation), 5.1–10.0 mm length	0.184	0.001
L. glyptocyma (Alum Bluff Group), 5.1–10.0 mm length	0.556	0.310

question of whether results can be compared among samples. Because the number and identity of prey and predators can differ among sedimentary environments, we do not compare drilling frequencies of taxa from different localities and ages. However, we argue that other measures such as the location of complete and incomplete drill holes and the percentage of incomplete drill holes can be compared in this case because (1) the taxa have a generally similar shape (Fig. 1), suggesting similarity of life mode; (2) a similar size range (5.1–10.0 mm length) was used for many analyses; (3) the ribs are comparable in shape across taxa; (4) the ratio of rib width to valley width is about equal regardless of rib size; (5) some analyses are within a taxon/sample; and (6) an overlapping range of drill hole sizes is present (Supplementary Table), suggesting that predator size may have been largely comparable. We assume that drilling gastropods

had a similar drilling behavior for the localities studied. The common gastropod drilling predators, naticids and muricids, were both present in all deposits (see above).

Incomplete Drill Holes and Placement of Drill Holes.—The percentage of incomplete drill holes tends to be lower in strongly ribbed species (Fig. 3). In contrast, Hingston (1985: Table 4) noted that the heavily ornamented bivalve *Placamen subroboratum* had a high percentage of incomplete drill holes relative to moderately ornamented to smooth bivalves from a Pliocene assemblage from SE Australia, but results were not standardized with respect to bivalve shape and size and the shell thickness without the ornamentation is not provided. Our results can be explained by the placement of drill holes: in stronger-ribbed species more drill holes tend to be placed between ribs, where the shell thickness to penetrate is less (Figs. 2, 4). Thus as rib strength
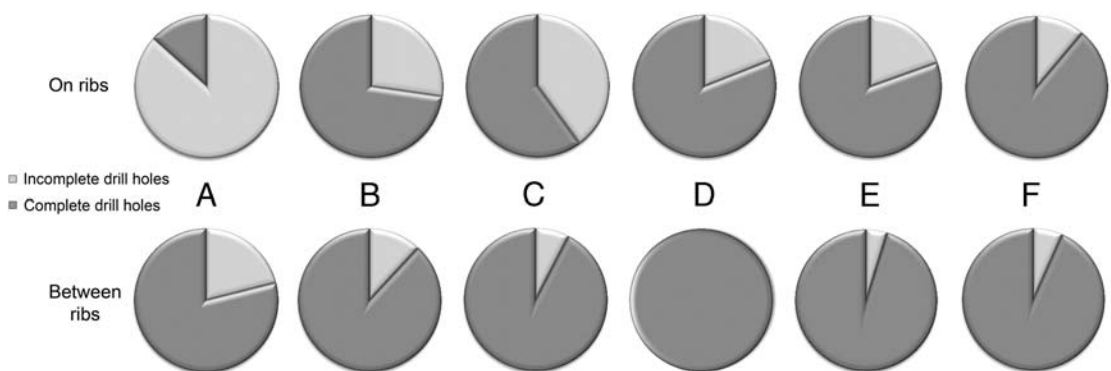

FIGURE 5. Proportions of incomplete and complete drill holes with the center on the rib and between ribs for eight samples with at least 30 drilled specimens. A–D, Specimens of all sizes included. A, *Lirophora athleta*, Jackson Bluff Formation, upper Pliocene, Florida (upper: 15 specimens; lower: 19 specimens). B, *L. athleta*, Tamiami Formation, Pliocene, Florida (22 and 42 specimens). C, *L. glyptocyma*, Alum Bluff Group (Oak Grove Sand), lower Miocene, Florida (20 and 92 specimens). D, *L. latilirata*, Waccamaw Formation, lower Pleistocene, North Carolina (121 and 138 specimens). E–F, Specimens with lengths from 5.1–10.0 mm. E, *Astarte goldfussi*, Breda Formation, middle Miocene, The Netherlands (82 and 21 specimens). F, *L. glyptocyma* (as above but with restricted length range of 5.1–10.0 mm) (9 and 30 specimens).

TABLE 4. *p*-values using the Mann-Whitney *U*-test comparing drill hole size of complete and incomplete drill holes. "Drill holes > Valleys" means that the outer diameter of the drill holes is greater than the width of the valley.

	All drill holes	Drill holes > Valleys
Astarte radiata	0.03	0.03
Astarte goldfussi	0.01	0.01
Lirophora latilirata	0.39	0.51

and spacing increased, gastropod predators selected the drill hole site with increasing stereotypy. This result suggests that natural selection favors gastropods that select drill hole sites between the ribs, thus saving time and energy, as rib strength increases.

Drill Hole Frequency in Astarte *spp.*—The stronger-ribbed shells of *Astarte goldfussi* have a significantly lower DF than the congeneric *A. radiata* from the same formation, horizon, and locality for the studied length range, implying that gastropods favored the smoother *A. radiata*. The similar shell shape and close phylogenetic relationship suggests that both species had a similar life mode and should have been equally susceptible to drilling. Both species are very common in the museum collections examined (>500 specimens), suggesting that relative abundance did not control drilling frequency. Therefore the lower DF in *A. goldfussi* likely can be attributed to the increased rib height (Fig. 1), given that the gastropods did not preferentially select a drill hole site between the ribs in either species (Fig. 4). This conclusion may be supported by the higher percentage of incomplete drill holes in *A. goldfussi*, although the difference is not statistically significant. Thus, the moderate-sized ribs in *A. goldfussi* appear effective against drilling predation because of the lack of stereotypy in drill hole site selection.

Drilling Success and Ribs.—Drilling is generally more successful between the ribs than on the ribs in most cases (Table 3, Fig. 5), as might be expected given the greater overall shell thickness on ribs. Greatly thickened bivalve shells are known to inhibit drilling (e.g., Vermeij 1978), and Kelley (1989) reported that increases in shell thickness in several Miocene bivalves correlated with decreases in successful drilling and increases in prey
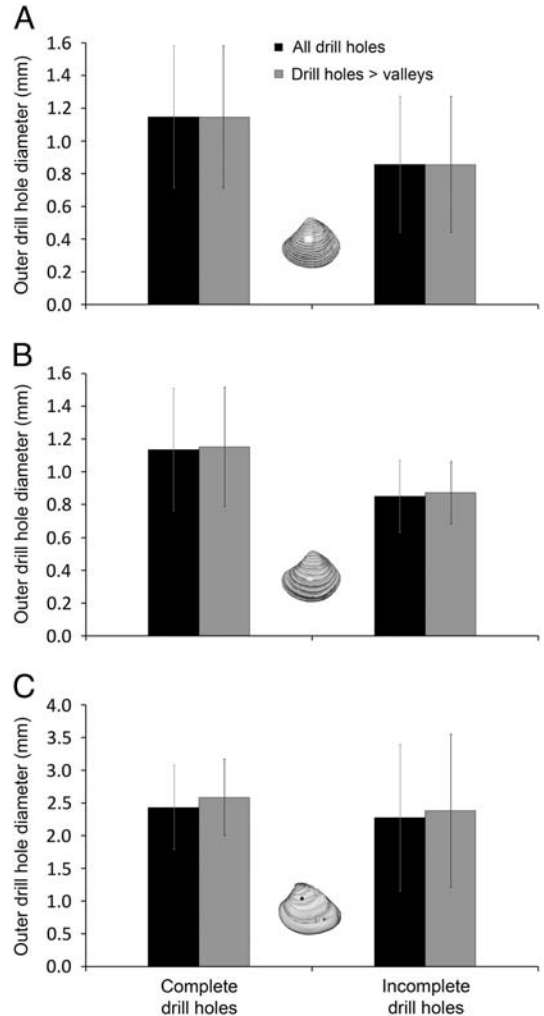

FIGURE 6. Mean outer drill hole diameter for complete and incomplete drill holes. A, *Astarte radiata*, 5.1–10.0 mm in length. B, *Astarte goldfussi*, 5.1–10.0 mm. C, *Lirophora latilirata* (North Carolina), all lengths. Error bars are ± 1 SD.

effectiveness. Addition of ribs provides a cost-effective means of increasing apparent shell thickness when drill holes are placed on ribs (see e.g. Ansell and Morton 1985). Fisher's exact tests on the percentages yield more significantly different results than tests based on the number of specimens, suggesting that more of these tests using the number of specimens would be significant if sample size were increased. Our result is based on Miocene–Pleistocene samples of *Lirophora* spp. and *Astarte goldfussi* from a variety of localities, suggesting that this pattern is consistent across time and space.

Drill Hole Size and Ribs.—Juvenile gastropods have been reported to drill prey from different phyla than those attacked by adult individuals (e.g., Maddocks 1988; Klompmaker 2012). Young gastropods also preyed upon different taxa within the same phylum and class compared to adults (Broom 1983, for bivalves). Drill hole position may also change during ontogeny of the driller (e.g., Calvet i Català 1992; Złotnik 2001). Specifically, Złotnik (2001) noted that when drilling *Corbula gibba*, large naticids displayed greater site selectivity than smaller individuals. The latter observation is in line with our results, as the outer drill hole diameter is usually significantly smaller for incomplete drill holes, suggesting that younger individuals produced these holes, which were often placed on ribs. Alternatively, adults of taxa with a small maximum size drilled preferentially on ribs, an explanation that seems less likely.

Drilling Behavior and Ornamentation.—Drill hole site selection by naticid gastropods has been studied widely and was reviewed by Kabat (1990), who concluded that no factor (shape of the prey, shell thickness, ornamentation, location of tissue, prey handling by predator, and prey size) solely determines the drill hole site for bivalves as a group. However, studies on individual bivalve prey have made strong cases for ornamentation playing an important role in determining the siting location and DF. For example, Ansell and Morton (1985) found that *Bassina calophylla* exhibiting pronounced, raised, sharp, concentric lamellae was not drilled by *Glossaulax didyma*. However, when the lamellae were removed this naticid gastropod did drill *B. calophylla*. They hypothesized that these lamellae may have confused predators by offering false valve margins, interfered with prey manipulation, and increased the perceived shell thickness. From their examination of empty shells from Mirs Bay (Hong Kong), Ansell and Morton (1985) further showed that drill holes were mainly located between the lamellae (their Fig. 5). This observation is in line with that of Anderson et al. (1991), who qualitatively noted that naticid drill holes were located between the concentric lamellae of *Chione cancellata*. Comparable results are also seen in most bivalves with smooth-topped ribs. Arua and

Hoque (1989) showed that 58.1% of the 308 drill holes in *Glans costaenodulensis* were located between the ribs, 82.2% ($n = 17$) of the drill holes in *G. triparticostata* were situated between the ribs, and 14.3% ($n = 14$) of the drill holes in *G. costaeirregularis* were located between the ribs. All species of *Glans* exhibit strong, seemingly smooth-topped radial ribs. One of the five (20%) drill holes in *Protonoetia nigeriensis* was found between the ribs (Arua and Hoque 1989), and *P. nigeriensis* showed less pronounced ribs (Arua 1986: Pl. 9, 10). Furthermore, based on a small sample of Miocene *Astarte anus*, Klompmaker (2011) noted that five of seven drill holes were located between the strong, smooth-topped concentric ribs.

These and other studies have not addressed the influence of space between ribs in detail. This factor becomes especially important here, because rib strength and rib spacing increase together (Fig. 2), raising the question as to which feature is most important in determining the siting of drill holes. Several aspects suggest that ornamentation strength is the most important trait. (1) We minimized the importance of rib spacing first by analyzing only those drill holes that fit between ribs and then by excluding drill holes that fit between ribs. In each case, the pattern of drill hole siting is similar to that when all sizes of drill holes are used (compare Fig. 4A with 4B; Table 2). (2) A higher DF is observed in the weaker ribbed of two *Astarte* species. Because no drill hole site is favored in these two species (Fig. 4A), rib spacing is not a complicating factor. However, for *Lirophora*, both rib strength and spacing may be important. (3) More incomplete drill holes occur on ribs than between ribs (Fig. 5). (4) Although Ansell and Morton (1985) studied a different type of concentric ornamentation, they found that the naticid *Glossaulax didyma* did not drill the bivalve *Bassina calophylla* when concentric lamellae were present, but did when lamellae were removed. Thus our results support the hypothesis that ornamentation influences the siting of drill holes, as siting between ribs is much more pronounced in bivalves with stronger concentric ribs. Spacing between ribs appears less important.

Function of Concentric Ornamentation.—Stanley (1970) suggested that concentric

ornamentation is resistant to burrowing by astartid and venerid bivalves, species of which are analyzed in this study. In a more detailed study of venerids, however, Stanley (1981) reported that concentric ribs that are asymmetrical in cross-section help in burrowing, whereas symmetrical concentric ribs do not. The latter arrangement decreases scouring, so specimens remain buried more effectively. All species studied here exhibit symmetrical concentric ribs, suggesting that they may have been buried shallowly with the ribs serving to reduce scour (however, rib size varies significantly among species, and ribs are generally more robust than those tested by Stanley 1981). Whether smooth-topped concentric ribs in bivalves function against durophagous predation has not been investigated in detail, although this interpretation was suggested cursorily by Alexander and Dietl (2003) and appears plausible given that other types of ornament are effective against predation (e.g., Stanley 1988). More specifically, radial ribs and ornamentation in general appear to deter durophagous predation for bivalves (Dietl et al. 2000; Alexander and Dietl 2003).

To determine whether a morphological characteristic that functions to deter predation is an adaptation or an exaptation, previous work has examined the first occurrence of the antipredatory trait. For example, conchiolin layers in corbulid and lucinid bivalves have been considered to be an antipredatory exaptation by Kardon (1998) and Ishikawa and Kase (2007), but Harper (1994) argued these layers were an adaptation to drilling predation. Both Harper (1994) and Kardon (1998) used the earliest occurrence of conchiolin in the fossil record to come to their conclusions. Concentric ribs in bivalves evolved in the Paleozoic and became more common in the Mesozoic (Stanley 1981; Vermeij 1995). Concentric rib-bearing astartid and venerid bivalves, species of which are studied herein, became diverse during the Jurassic and Cretaceous, respectively (Cox et al. 1969; Paleobiology Database 2013). Although *Lirophora* spp. are known from the Cenozoic only (e.g., Cox et al. 1969), Cretaceous venerids show weak to moderate-sized concentric ornamentation (e.g., Wade 1926; Imlay 1961; Sealey and Lucas 2003). *Astarte* is

known from the Paleozoic and became speciose in the Jurassic (Paleobiology Database 2013); moderate-sized concentric ribs, comparable to those in the Miocene *Astarte* spp. studied here, were present since at least the Triassic for this lineage (McRoberts and Blodgett 2000; Yin and McRoberts 2006). Conversely, drilling frequencies were generally low in the Neoproterozoic, Paleozoic, and Mesozoic, but were higher in the Late Cretaceous–Cenozoic (Vermeij 1987; Kelley and Hansen 1993, 2003; Kowalewski et al. 1998; Huntley and Kowalewski 2007).

Ishikawa and Kase (2007) used absence of a temporal trend, among other reasons, as an argument that conchiolin layers were an exaptation to drilling predation. Similarly, our analysis shows that rib strength of North American *Astarte* remained stable during the Jurassic–Paleogene as drilling gastropods diversified. All of the above evidence suggests that smooth-topped, symmetrical ribs did not evolve as an anti-predatory trait against drilling predation. Our results show that, when ribs are moderately strong and when drill holes are placed on top of ribs, concentric ribs can be effective against drilling predators. Furthermore, Stanley (1981) suggested that concentric ribs in bivalves are adaptations to burrowing and/or stabilizing the sediment. It is also possible that these ribs evolved as an adaptation to durophagous predation. In sum, the concentric ribs herein can be viewed as a likely example of exaptation with regard to drilling predation. Smooth-topped, symmetrical concentric ribs can thus fulfill a variety of functions.

Our conclusion that smooth-topped concentric ribs are likely an antipredatory exaptation with regard to drilling predation would be strengthened if phylogenies were available for these species (see Blackburn 2002). Nevertheless, claims concerning adaptations versus exaptations by Kardon (1998), Ishikawa and Kase (2007), and Harper (1994) were made without a phylogenetic context, most likely because of the lack of phylogenies at low taxonomic ranks. Other examples without a phylogenetic framework hypothesizing that ornamentation evolved through adaptation to drilling predation include work on Paleozoic brachiopods (Leighton 2001, 2003). Adaptation against durophagous predators through

ornamentation on bivalves was suggested by Dietl et al. (2000) and Han et al. (2008), but only the former made use of a phylogenetic framework (i.e., "lineages").

To our knowledge, this study is one of the first examples investigating the effectiveness of drilling predation across prey with a range of the same type of ornamentation. This type of study could be extended to asymmetrical concentric ribs, radial ribs, spines, and other types of ornamentation in a variety of mollusks. Data on the first appearance and abundance of these characters may help determine whether these ornaments are exaptive or adaptive traits or ineffective against drilling and/or durophagous predation in bivalves and other marine invertebrates. Whether ornamentation such as concentric ribs played a role in drill hole site selection by early representatives of naticid and muricid gastropods during the late Mesozoic could also be addressed by other studies. If a different stereotypic drilling pattern or no stereotypy at all were found, then the effectiveness of ribs in deterring drilling predation might have been different during that time.

Conclusions

1. The percentage of drill holes located between the ribs on bivalve species with concentric ribs increases with increasing rib strength, whereas the percentage of drill holes on top of ribs decreases. This result supports the hypothesis that ornamentation influences the siting of drill holes, as siting between ribs is much more pronounced in bivalves with stronger concentric ribs. Thus, natural selection favors gastropods that select drill hole sites between the ribs.
2. The lack of stereotypy in drill hole site selection suggests that the moderately sized ribs in *Astarte goldfussi* were effective against drilling predation.
3. The percentage of drill holes that are incomplete is generally lower in strongly ribbed species.
4. The proportion of drill holes that are located on top of ribs is greater for incomplete than complete holes, implying that ribs can be effective against predators in these cases.

5. The outer drill hole diameter is usually significantly smaller for incomplete drill holes, suggesting that younger individuals produced these holes.
6. Moderately strong ribbing considered herein serves as a likely exaptation against drilling predation, especially when drill holes are placed on top of ribs.
7. The functions of smooth-topped concentric ribs are manifold, as they can not only deter durophagous and drilling predation, but also serve to stabilize the bivalve in the sediment.

Acknowledgments

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