

SHAPE DIFFERENCES AMONG BOREHOLES DRILLED BY THREE SPECIES OF NATICID GASTROPODS

MELISSA GREY^{1,3}, ELIZABETH G. BOULDING¹ AND MICHAEL E. BROOKFIELD²

¹Department of Zoology, University of Guelph, Guelph, Ontario, N1G 2W1 Canada;

²Department of Land Resource Science, University of Guelph, Guelph, Ontario, N1G 2W1 Canada;

³Present address: Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, British Columbia, V6T 1Z4 Canada

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ABSTRACT

Naticid gastropods leave a record of predation in the form of characteristic countersunk circular boreholes. We fed bivalve prey to naticids to test whether the ratio between the inner and outer borehole diameter differed among three Recent naticid species: *Euspira heros*, *E. lewisii* and *Neverita duplicata*. Fossil shells from a Miocene-aged assemblage, containing naticids previously identified as *E. heros* and *N. duplicata*, were also included in our analyses. Ratios of the inner to outer diameters of naticid boreholes in bivalve shells showed that there were significant differences in borehole shape between *E. heros* and the two other Recent species. We found no significant differences between the ratios of *E. lewisii* and *N. duplicata*; however, a principal component analysis showed that boreholes distinctly cluster according to species. The Miocene boreholes were also distinct from the Recent, indicating that the Miocene naticids may be a separate species from *E. heros* and *N. duplicata*. We have shown that there is a species-specific component to borehole geometry. This may have important implications for palaeobiological studies, because the index of borehole functionality, previously described as an inner to outer borehole ratio of 0.5 for all naticids, may differ between species.

INTRODUCTION

The characteristic countersunk boreholes of naticid gastropods in fossil and Recent assemblages provide direct evidence of naticid feeding and allow quantification of predator-prey relationships. Much of the research on drilling mechanisms in both naticid and muricid gastropods was synthesized by Carriker (1981). Naticid boreholes can give information on predator size, predator selectivity and predator behaviour (Kitchell, 1986) and studies have used borehole characteristics for research on co-evolution (Kelley, 1992), prey selection (Kelley, 1988, 1991; Kitchell *et al.*, 1981) and escalation (Kelley & Hansen, 1996). Recent studies have documented cases where prey shell characteristics can influence borehole morphology (see Kowalewski, 2002: table 3). However, no study has hitherto shown that different naticid species differ in borehole morphology.

The morphologies of naticid boreholes have been used to measure 'prey effectiveness'. Prey effectiveness, defined as the percentage of incomplete and non-functional boreholes (see Kelley & Hansen, 1996), is a statistic that can provide a conservative estimate of the potential for antipredatory selection (Vermeij, 1983). Kitchell *et al.* (1986) described a functional borehole as one that has an inner borehole diameter to outer borehole diameter ratio greater than 0.5. Borehole ratios less than 0.5 were classified as non-functional because the inner hole would not be large enough for the naticid's proboscis to penetrate and feeding could not occur (Kitchell *et al.*, 1986). This index of 0.5 was based on experimentation with one naticid species, *Neverita duplicata* (previously called *Polinices duplicata*), and we hypothesize that the index may change for different naticid species. Other researchers have also questioned the validity of this statistic (see Harper, 1994; Hoffmeister & Kowalewski, 2001). There is clearly a need for further investigation.

Previous studies of borehole morphology have indicated that there may be shape differences in boreholes between naticid

species. Berg & Porter (1974) and Berg & Nishenko (1975) found that holes made by *N. duplicata* were significantly smaller than those made by *Euspira heros* of the same shell length (Berg & Porter, 1974). In addition, *E. heros* and *N. duplicata* bored into different areas of the shell in each of their prey species (Berg & Nishenko, 1975). In contrast, Stanton, Powell & Nelson (1981) found no differences between the borehole size of three species of naticids (*Natica aratus*, *N. sp.*, and *Sinum bilix*). All of these studies were based exclusively on visual comparisons rather than on quantitative morphometric analyses.

We investigated whether different species of naticids drill differently shaped boreholes. Recognized geometric differences in boreholes between species of naticids will help to elucidate whether borehole functionality for every species of naticid should be based on the 0.5 index. We predict that, if there is a species-specific component to borehole morphology, then: (1) ratios of inner to outer borehole diameter should be different for different naticid species; (2) principal component scores for borehole traits should form distinct clusters in morphospace according to species; and (3) borehole variation between naticid species should be greater than borehole variation within a naticid species preying on different prey taxa.

MATERIAL AND METHODS

Recent material used for this study was obtained from feeding experiments and beach collections. *Euspira heros* and *E. lewisii* were maintained for 6 months at the University of Guelph Aqualab with coarse sand (10 cm deep) and re-circulating seawater (11°C; 30 ppt). The maximum length of each snail was measured with electronic calipers to the nearest 0.1 mm. *Euspira heros* ranged in length from 30 to 60 mm and *E. lewisii* ranged from 50 to 100 mm. Snails were fed native littleneck clams (*Protothaca staminea*), a common prey of *E. lewisii*, that ranged in size from 20 to 60 mm. Beach collections were obtained from G. Deitl, who collected shells from Wrightsville Beach, an exposed sandy beach on the Atlantic Ocean, in Wilmington, NC, USA. Boreholes in the surf clam, *Spisula*

Correspondence: M. Grey; e-mail: mgrey@eos.ubc.ca

solidissima, in this collection were made by *Neverita duplicata*, the sole naticid predator in the area (G. Deitl, personal communication).

Boreholes in bivalves from a fossil shell bed of Upper Miocene age (5–8 million years old), collected by M. Brookfield, were also included in the analysis. The shell bed (up to 1 m thick) occurs in Miocene Lithostratigraphic Unit 24, in the silty clays of the Upper Miocene St Mary's Formation at Chesapeake Ranch Club on the south shore of Chesapeake Bay, Maryland, USA (Kidwell, 1989). This bed is dominated by disarticulated but frequently undamaged bivalve valves (as well as *Turritella*), which frequently contain naticid boreholes. The bored bivalve taxa are dominated by *Dallarca idonea*, *Bornia mactroides* and *Mercenaria mercenaria*. There are two naticid species present in nearly equal proportions, *N. duplicata* and *E. heros*, ranging from very small juveniles to mature adults (Vokes, 1957). The identity of these species is debatable, however (see Deitl & Alexander, 2000), and their inclusion in our study may help to reveal whether the fossil naticid species are indeed *N. duplicata* and *E. heros*.

Borehole comparisons among naticids

Borehole dimensions (inner and outer borehole diameter) were measured with electronic calipers for all Recent and fossil material. Miocene material, from an assemblage possibly containing both *N. duplicata* and *E. heros*, were included in the analysis in order to test whether the fossil species would cluster with their Recent counterparts, or if they would cluster together. Fossil holes were considered as one taxonomic unit because we were uncertain of the true identity of the naticid species responsible.

Morphometric differences between boreholes of the three Recent naticid species and those from the fossil assemblage were determined by using a variety of tests. We first plotted regressions of the inner borehole diameter (IBD) versus outer borehole diameter (OBD) and tested for differences among slopes using a Tukey multiple comparison test. Ratios of IBD to OBD for each species were compared using a Kruskal–Wallis multiple comparison test. We also computed a principal component analysis (PCA) for the morphological variables, IBD and OBD, to determine if the principal component scores formed distinct clusters in morphospace for different species. A PCA on these two variables was performed because it allows separation of variation due to size from variation due to shape (Humphries *et al.*, 1981). The PCA was computed by the Primer package version 5 (Clarke & Gorley, 2001).

Comparisons of borehole shape among prey species

The prey taxa used in our experiments were not kept constant; the beach assemblage of *N. duplicata* fed on *Spisula solidissima* whereas our laboratory experiments with *E. heros* and *E. lewisii* fed on *Protothaca staminea*. We therefore tested whether a particular naticid species bores differently shaped holes in different species of prey. A Kruskal–Wallis test was used to compare the ratio of outer borehole diameter to inner borehole diameter produced by *E. lewisii* when boring four common bivalve species (*P. staminea*, *Tresus nuttallii*, *Macoma nasuta* and *Saxidomus giganteus*). These data were obtained from field collections of bored bivalve shells near Bamfield Marine Sciences Centre on the west coast of Vancouver Island, BC, where *E. lewisii* is the sole naticid predator present.

RESULTS

Regression lines of outer borehole diameter versus inner borehole diameter differed for some naticid species (Fig. 1;

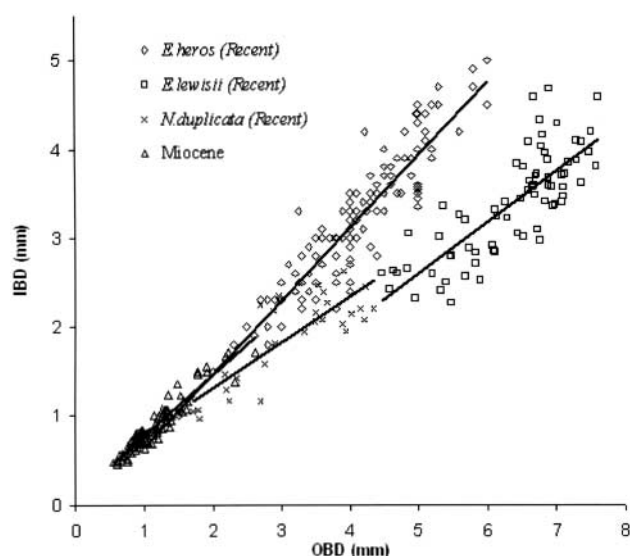


Figure 1. Shape differences of borehole among three recent species of naticids, *Euspira heros*, *E. lewisii* and *Neverita duplicata*, and data from one Miocene fossil assemblage. Inner borehole diameter plotted against outer borehole diameter.

Table 1). There was a strong correlation between the outer and inner borehole diameters for all species studied, with R^2 values ranging from 0.63 to 0.90 (Table 1). Tukey multiple comparisons showed significant differences in slopes between *E. heros* and *E. lewisii* and also between *E. heros* and *N. duplicata*, but not between the other pairs of taxa (Table 2).

Results from the Kruskal–Wallis test showed significant differences ($P < 0.001$) in ratios of IBD to OBD between *Euspira heros* and *E. lewisii* and between *E. heros* and *Neverita duplicata* (Table 3). No significant differences were detected between the boreholes of *E. lewisii* and *Neverita duplicata* or between *E. heros* and the Miocene sample. The average ratio of inner (IBD) to outer borehole diameter (OBD) for the naticid species ranged from 0.53 to 0.78 and the overall range of all ratios for all species was 0.41–0.99 (Table 3). Based on Kitchell *et al.*'s (1986) non-functionality index of 0.5, nearly 30% of boreholes from feeding experiments with *E. lewisii* and 10% of those from the beach assemblage of *N. duplicata* would be considered non-functional. None of the drill holes from the Miocene and Recent *E. heros* collections would be considered non-functional.

Principal component analysis revealed that size (PC1) represented 94.8% of the variance, while shape (PC2) represented 5.2% (see Table 4 for loadings on variables). The principal component scores formed clusters in morphospace according to species and ordination plots show reasonable separation among species (Fig. 2). *Euspira lewisii* was the most distinct from the rest of the taxa, while the Miocene boreholes along the axis of PC1 did not overlap in the morphospace with *E. heros* or *N. duplicata*, likely because of size differences (Fig. 2).

Table 1. Linear model for regression lines of inner borehole diameter versus outer borehole diameter for *Euspira heros*, *E. lewisii*, *Neverita duplicata* and a Miocene assemblage.

Naticid species	N	Slope of regression line	Y intercept	R^2
<i>E. heros</i>	181	0.8222	-0.1731	0.87
<i>E. lewisii</i>	76	0.5802	-0.3054	0.63
<i>N. duplicata</i>	30	0.5137	-0.2821	0.65
Miocene	90	0.6835	0.0912	0.90

Table 2. Results from the Tukey multiple comparison test (Zar, 1999) for slope of regressions of inner borehole diameter versus outer borehole diameter for *Euspira heros*, *E. lewisii*, *Neverita duplicata* and a Miocene assemblage. See Zar (1999: appendix B, table B.5) for critical values of the q distribution.

Slope comparison	N	q
Miocene vs <i>N. duplicata</i>	120	3.12
Miocene vs <i>E. heros</i>	271	3.03
Miocene vs <i>E. lewisii</i>	166	1.77
<i>N. duplicata</i> vs <i>E. heros</i>	211	4.18*
<i>N. duplicata</i> vs <i>E. lewisii</i>	106	0.87
<i>E. heros</i> vs <i>E. lewisii</i>	257	7.12**

*Significant at 0.05 level, **significant at 0.001 level.

Comparisons of borehole shape among prey species

A Kruskal–Wallis test showed no significant differences ($P = 0.306$) among the shape of boreholes produced by *E. lewisii* on four different prey species (Table 5). These results should be viewed with caution given our small sample sizes. However, the mean IBD/OBD ratios vary in a narrower range (0.04; Table 5) across different prey species than when compared with IBD/OBD ratios across different naticid species (0.25; Table 3).

DISCUSSION

Our results indicate that there are differences in borehole shapes between some naticid species. This agrees with the qualitative results of Berg & Porter (1974) and Berg & Nishenko (1975) and quantitative results of Grey (2001) who found differences in borehole diameter with predator shell length between *E. heros* and *N. duplicata*. Our results, indicating that the slopes of the regression lines for inner and outer borehole diameter for these two species are significantly different, support their findings. The slopes for the other pairs of taxa that were not significantly different closely match our results for the Kruskal–Wallis test, indicating that not all species can be distinguished from one another based on their boreholes.

We were unable to detect shape differences between boreholes from *E. lewisii* and *Neverita duplicata* with the Kruskal–Wallis test; however, the principal component analysis revealed that all three Recent naticid species formed distinct clusters in morphospace and that *E. lewisii* was the most distinct. Results from these two tests may not agree because the separation of *E. lewisii* was good along the ‘size’ axis, or PC1 (Fig. 2). Future studies that include additional morphological variables, such as the borehole angle, would probably increase the

Table 3. Results of the Kruskal–Wallis test on borehole ratio between different naticid species. Non-parametric multiple comparisons (Zar, 1999) with different letters are significantly different ($P < 0.001$). Non-parametric multiple comparisons with same letters are not significantly different ($P > 0.05$).

Naticid species	N	Ratio range of IBD:OBD	Mean IBD/OBD	Mean rank	Multiple comparison
<i>E. heros</i>	181	0.57–0.99	0.78	236.1	a
<i>E. lewisii</i>	76	0.41–0.68	0.53	47.4	b
<i>N. duplicata</i>	30	0.43–0.83	0.61	96.0	b
Miocene	90	0.59–0.91	0.77	234.9	a

Table 4. Loadings of variables, inner borehole diameter and outer borehole diameter, on the first two principal components.

	PC1	PC2
IBD	0.707	–0.707
OBD	0.707	0.707

capacity to discriminate species-related differences in borehole morphology.

The Kruskal–Wallis test did not detect differences in borehole ratio between *E. heros* and the Miocene sample, suggesting that fossil naticids bored similarly shaped holes to those of the Recent *E. heros*, or that all the holes we measured were indeed from the fossil *E. heros* species. Results from the PCA, however, showed that the holes from the fossil naticid species appeared to group more closely to each other than to their possible Recent counterparts and this suggests that the Miocene boreholes are from one species of naticid that is smaller than all of the Recent species. This supports Deitl & Alexander (2000), who indicated that the fossil naticids may not be the same as the Recent species.

Prey shell characteristics, such as prey size, represent confounding factors in this analysis because the prey species were not kept constant. As summarized by Kowalewski (2002: Table 3) prey shell factors such as thickness, structure, hardness, ornamentation, geometry and taphonomic alteration can affect drill hole morphology. These factors were not constant throughout our experiment and it is possible that differences in borehole structures may be due to the prey shell characteristics rather than naticid drilling mechanisms. Indeed, Kitchell *et al.* (1981) showed that borehole morphology in a prey shell changes with the depth of penetration. Our results indicate that, although there is slight variation of borehole morphology within a naticid species, the variation among naticid species is much greater. This shows that there is a species-specific component to borehole geometry.

Our research has important implications for the calculation of the ‘prey effectiveness’ statistic, where a ‘non-functional’ borehole may be a key factor. Kitchell *et al.*’s (1986) definition of a non-functional borehole (IBD:OBD < 0.5) is based solely on experimentation with *N. duplicata*. We have demonstrated that different naticid species can have different ratios of inner to outer borehole diameter; therefore, non-functionality in other species of naticids is probably different from the common index

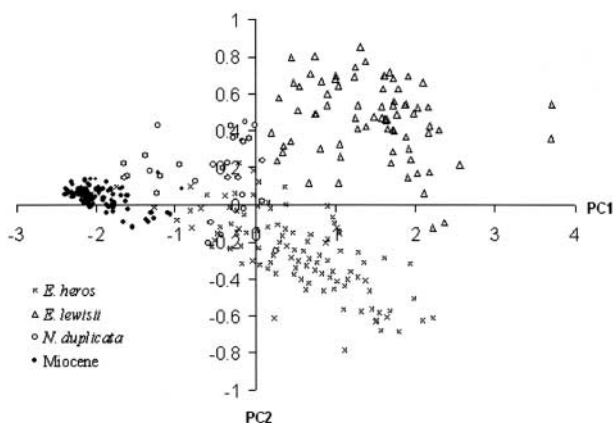


Figure 2. Principal component analysis of borehole shape. Plot of the scores on the first two principal components. PC1 represents size variation, while PC2 represents shape variation.

Table 5. Results of Kruskal–Wallis test on borehole ratio between different prey taxa. Non-parametric multiple comparisons (Zar, 1999) with different letters are significantly different ($P < 0.001$). Non-parametric multiple comparisons with same letters are not significantly different ($\alpha > 0.05$).

Prey species	N	Mean IBD/OBD	Mean rank	Multiple comparison
<i>Protothaca staminea</i>	20	0.69	21.20	a
<i>Tresus nuttallii</i>	6	0.67	22.17	a
<i>Macomma nasuta</i>	10	0.68	23.30	a
<i>Saxidomus giganteus</i>	11	0.65	30.73	a

of 0.5. For each naticid species it will be important to determine a non-functionality index based on laboratory experimentation.

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