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Supplementary Material for

Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems

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Supplementary Materials for

Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems

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Databases S1 to S2 as zipped archives: Database 1, Database 2

Materials and Methods

We collected linear mean, maximum, and minimum body size measurements of individuals and/or the summary statistics of individuals in a sample of prey items and the mean, maximum, and minimum outer drill hole diameter for Phanerozoic single taxon occurrences per type of inferred driller (parasite, predator sensu stricto, etc.) from the literature published between 1861 and 2016. Although a variety of prey items are drilled in the fossil record (*8*, *38–42*), current analyses are restricted to marine brachiopod and molluscan prey (362 occurrences) because these benthic, shell-bearing clades are dominant taxa in the marine fossil record (*9*), comprise 80% of the Phanerozoic drill-hole data, are of comparable body size, contain the longest and most complete stratigraphic record, and mollusks and some brachiopods are important prey of predatory drillers today (*38*, *43–46*). Height or thickness of articulated bivalves and brachiopods, respectively, were typically unavailable, so we were unable to calculate precise shell volumes. Rather, we used lengths and widths to approximate shell size (*47*, *48*). Data were collected using reported drill-hole and prey sizes (means typically), extracting data from diagrams, and measuring drilled specimens from monographs and articles for geological periods with limited data. All taxa with at least one drilled specimen were used for analyses to ensure

maximum possible sample sizes. We used specimens with lengths or widths > 2.0 mm because small shells are preferentially destroyed in lithified sediments relative to unlithified sediments (*49*), which become more common in the Cenozoic (*50*). Furthermore, mollusks and brachiopods of < 2.0 mm in size are inconsistently included in studies on drilling predation (*51*). Latitudes and longitudes per occurrence were obtained using Google Earth (accuracy within 1° for 95% of data). Where possible, lithology was scored as unlithified or lithified using PBDB data and our own inferences. Numerical ages for drilled shells were estimated as the midpoint of the time unit, mostly stages, to which drill holes were ascribed following the ICS Timescale 04/2016.

Evolutionary models from R package PaleoTS 0.5-1 (*11*, *52*, *53*) were run on $\log_{10}$-transformed per-taxon occurrence period-level variables, which included mean drill-hole diameters, mean drilled shell areas (= π x 0.5length or height x 0.5width), and mean ratios of drill-hole area (π x 0.5 x drill-hole diameter^2) / prey shell area. The preferred "joint" parameterization was used and variances were not pooled across samples (*11*, *48*). The length of the time series allowed usage of up to four models using PaleoTS 0.5-1: directional trend, unbiased random walk, stasis, and strict stasis (*11*, *53*), although we have used complex models as well (see below). Data was not weighted per prey sample size to reduce possible effects of uneven sampling per taxon.

To test the robustness of the resulting temporal trend of the percentage of shell area drilled, a variety of sensitivity analyses were carried out, using different metrics, taxonomic and ecological subsets of the data, and complex models. The following variants have been used: (1) Instead of the percentage of shell drilled, the percentage of shell length drilled (Table S5) and shell width drilled (Table S6) were used; (2) Gastropods + brachiopods (Table S7) and bivalves + brachiopods (Table S8) were used to test the influence of individual clades; (3) The analyses were restricted to North America to test whether patterns were caused by fortuitous mixing of global data (Table S9). Other continents did not yield sufficient data per period and temporal coverage. For example, Eurasia yielded data from only the Devonian onward, but only the Triassic, Cretaceous, and Paleogene contained > 10 data points for the percentage of shell drilled; (4) The median and standard error were used as inputs for the likelihood-models instead of the mean and variance (Table S10); (5) The mid-point of periods instead of the age of the median data point were used (Table S11); (6) As lithification also preferentially destroys shell sizes of 2 – 5 mm relative to unlithified sediments, but much less so than for shells < 2 mm in size (*49*), the analyses were also restricted to specimens > 5 mm for either length or width (Table S12). For comparison, we also analyzed the data without size restrictions (Table S13); (7) We use 'predator' in a broad sense (*14*, *54*) because differentiating between drill holes produced by predators *sensu stricto* and parasites can be difficult in the early Mesozoic and Paleozoic (*55*, *56*) and both predators and parasites have a negative effect on the prey. The analyses were restricted to inferred *predatory* drill holes only (Table S14); (8) The minimum number of specimens per data point was doubled to two (Table S15). Increasing this number to three lowered the number of data points per bin to ≤ 6 for 5/11 bins including two bins without data, which was deemed insufficient for meaningful analyses; (9) The Paleobiology Database was used to obtain the inferred paleoecology (motility and life habit) per taxon after which analyses were run for stationary and epifaunal taxa separately (Tables S16–S17). Data for non-stationary and infaunal prey were too sparse for meaningful analyses (Figs. S12–S13);

(10) In addition to using an ellipse to approximate shell area, the area of the shell drilled was calculated using two other methods. First, the area of a cone to approximate shell surface area of gastropods and the area of a single valve for brachiopods and bivalves was doubled to approximate exposed total shell area for each taxon (Table S18). Secondly, bivalve and brachiopod shell area was approximated as an ellipsoid with valve height estimated by (width + length) / 2, which is not a conservative estimate for height (Table S19); and (11) A minimum of 14 bins is required for complex evolutionary models (*11*) to run in PaleoTS. Because the Cenozoic has relatively many data points per bin, the periods were subdivided into epochs to expand the number of time bins so that also complex models could be run (Table S20).

To test whether the temporal trend of the percentage of shell area drilled could be due to taxonomic mixing of the prey clades (brachiopods, bivalves, and gastropods) or preferential dissolution of aragonitic mollusks (*13*), two strategies were chosen. First, we compared the drill-hole size / shell size between brachiopod and bivalves within Permian (*29*, *57*) and modern assemblages (*30*). This method eliminates the time component in the most direct way. To our knowledge, these were the only assemblages suitable for this analysis. Secondly, a permutation test was designed to simulate the expected trajectory of predator-prey size ratios if the sizes of drill holes did not change through time *within* the clades (that is, if the trajectory was entirely an artifact of replacement among the prey clades). We carried out 1000 iterations of this permutation procedure, and used the paleoTS::fit4models() function to evaluate relative support for different models for each permutation.

Furthermore, the literature of modern, extant organisms was surveyed for direct evidence of driller lengths, driller widths, and drill-hole diameters supplemented with a single Mississippian platyceratid gastropod atop a drill hole in a crinoid (*58*) for which only the gastropod width could be estimated. The identity of the modern drillers was either based on direct field or experimental observations of known predators. Data were collected using reported drill-hole and prey sizes, extracting data from diagrams, and measuring the size of figured individual predator specimens and the drill-hole diameters they produced. Most data are based on singly drilled specimens (98%); for the others, the available means were used if insufficient data was available for single specimens. Octopods were excluded because their size is typically expressed as a weight instead of shell width and/or length (*44*, *59*, *60*). A reduced major axis regression line was fit through the logged data and 95% confidence intervals were estimated by a bias-corrected and accelerated (BCa) bootstrap method (1000 iterations). Bootstrap distributions of slope and r-square values were derived by resampling with replacement bivariate sets of observations. The confidence interval estimates were based on the bias-corrected and accelerated (BCa) bootstrap using jackknife approximation (*61*), an approach which adjusts bootstrap distribution for both bias and skewness. This approach was implemented using a custom-made function in R. Shell length was used because most data were available for this measure of size. However, we also ran the analysis for drillers' shell width, shell lengths $\geq$ 1 mm, for marine taxa only, and for predatory drill holes only. Insufficient data was available for parasites for a separate analysis.

We used drill-hole diameter as a proxy for predator size in deep time. This relationship is suggested by results herein using drillers from a variety of phyla, but also for multiple extant gastropod drilling species over a range of shell sizes (*62–65*). The size

of the driller is positively correlated with its boring organ, which, in turn, is positively correlated with the drill-hole diameter (*38*, *66*, *67*). Furthermore, there is no significant relationship between prey size and drill-hole size for individual specimens of drillers (*68*). Finally, multiple studies suggest that there is no relationship between taphonomic condition and the presence of drill holes (*69–71*).

The size of drilling predators is considered herein a correlative for power (strength and speed) or predators. This proxy is used here to test a key tenet of the hypothesis of escalation: predators became more powerful over time. Although drilling rates (mm/hr) are independent of predator size (*62*, *72*), larger drilling predators are faster (*73*, *74*) and thus more able to successfully pursue prey, should have an easier time subduing prey once the prey is reached, and ingest prey faster through the larger hole (*72*) for the same prey size and species.

Finally, using the primary literature, shell lengths (or heights) and widths were collected from the holotypes or largest syntypes of Late Cretaceous – Cenozoic fossil species of the type genera of the two best-known and extant predatory drilling families, *Natica* of the Naticidae and *Murex* of the Muricidae, as listed in the Paleobiology Database (11/01/2016). The largest syntype likely approaches what would have been the holotype size (*75*). We also collected such data from hypothesized Paleozoic – Triassic predatory drilling species suggested in the literature minus those species found attached to echinoderms because these species, typically platyceratids, can drill but are considered parasitic (*58*, *76*, *77*). The Mann-Whitney test was used to compare the $\log_{10}$ shell volumes ($\pi \times (\text{shell radius})^2 \times \text{shell height}/3$).

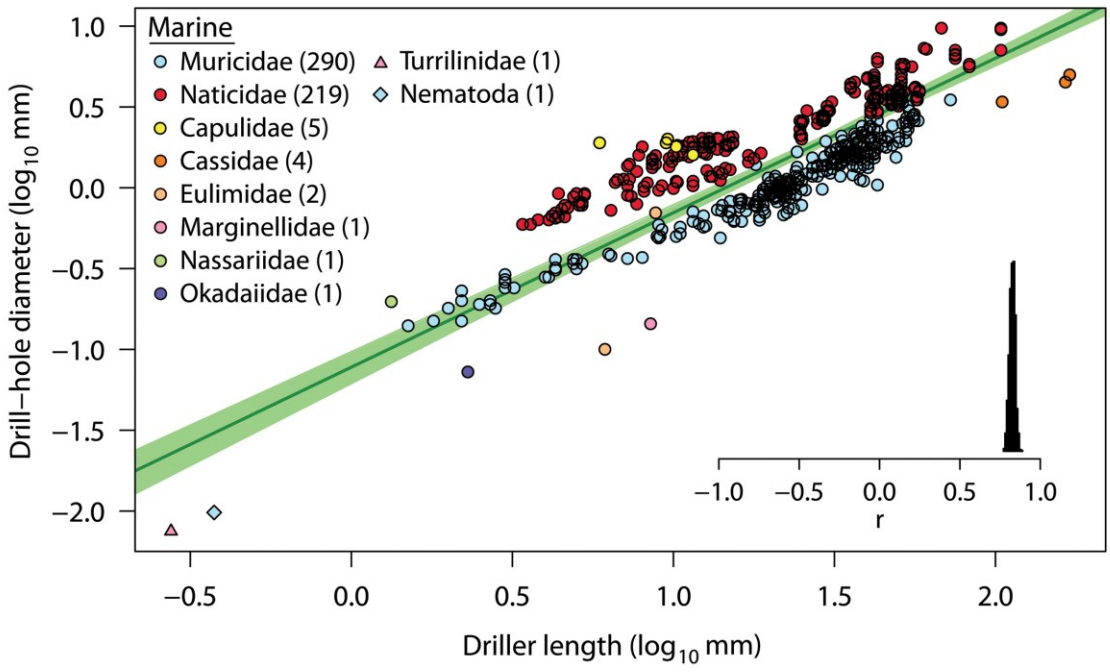

Fig. S1. Re-analysis of drill-hole size versus predator shell size relationship for data limited to exclusively marine clades of drilling predators. Reduced major axis regression line supplemented by 95% bootstrapped confidence intervals and bootstrapped r-values in histogram (both 1000 iterations) (*10*). Log_{10} slope = 0.96, intercept: -1.11.

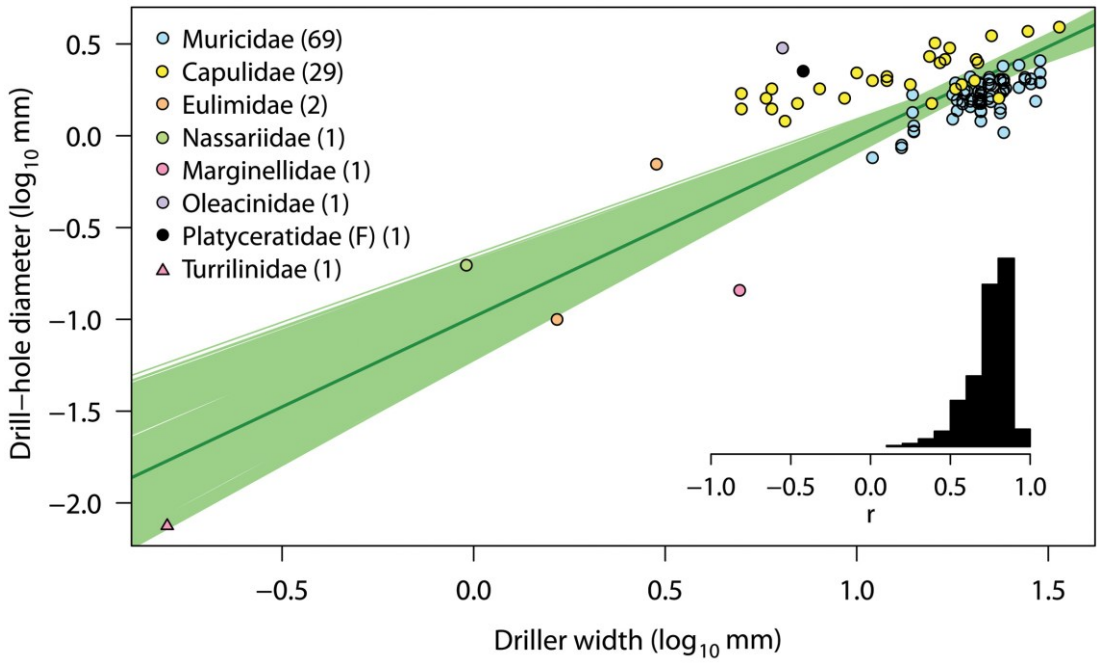

Fig. S2. Re-analysis of drill-hole size versus predator size relationship using shell width for modern drilling clades and a single fossil occurrence (*58*)**.** The fossil is a platyceratid gastropod and is indicated by black circle near green square. Reduced major axis regression line supplemented by 95% bootstrapped confidence intervals and bootstrapped r-values in histogram (both 1000 iterations). Log_{10} slope = 0.98 intercept: -0.99.

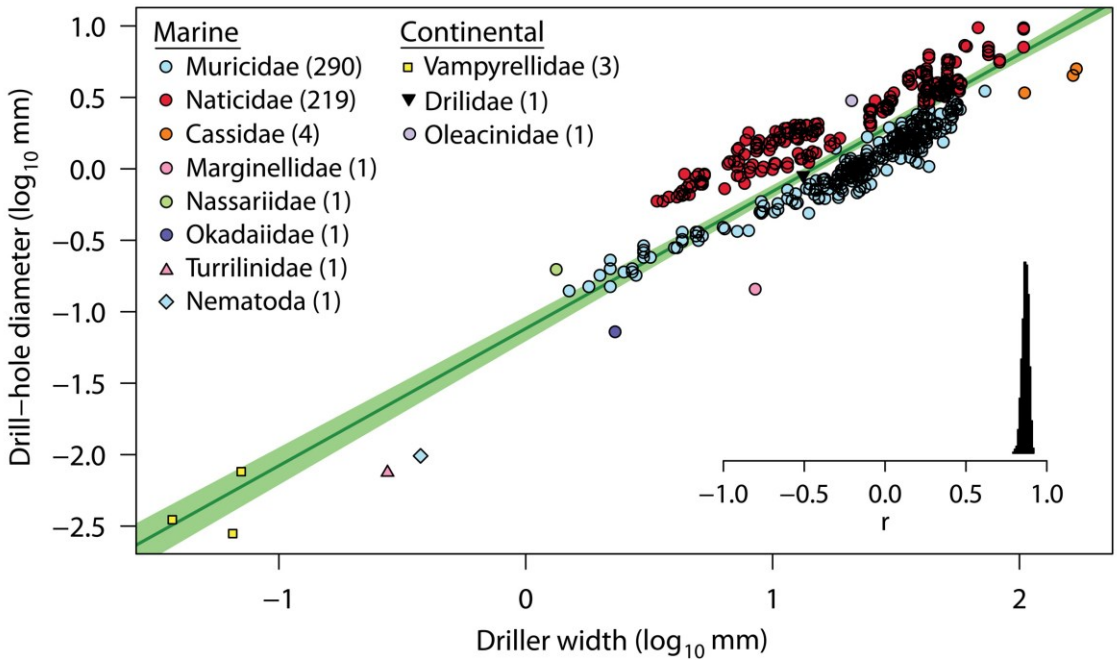

Fig. S3. Re-analysis of drill-hole size versus predator shell size relationship for data limited to exclusively predatory drilling clades. Reduced major axis regression line supplemented by 95% bootstrapped confidence intervals and bootstrapped r-values in histogram (both 1000 iterations). Log_{10} slope = 0.96 intercept: -1.12.

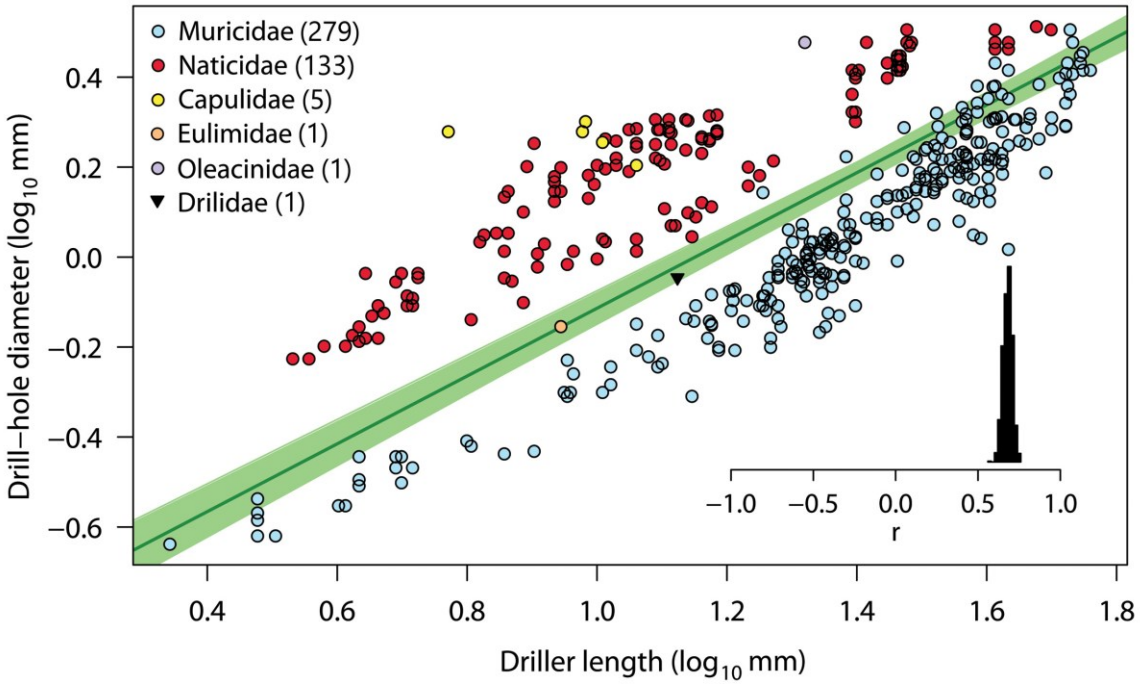

Fig. S4. Re-analysis of drill-hole size versus predator shell size relationship for data limited to drill-hole diameters of 0.2–3.3 mm. This is the range over which drill-hole size medians changed across the Phanerozoic. Reduced major axis regression line supplemented by 95% bootstrapped confidence intervals and bootstrapped r-values in histogram (both 1000 iterations). Log_{10} slope = 0.75 intercept: -0.87.

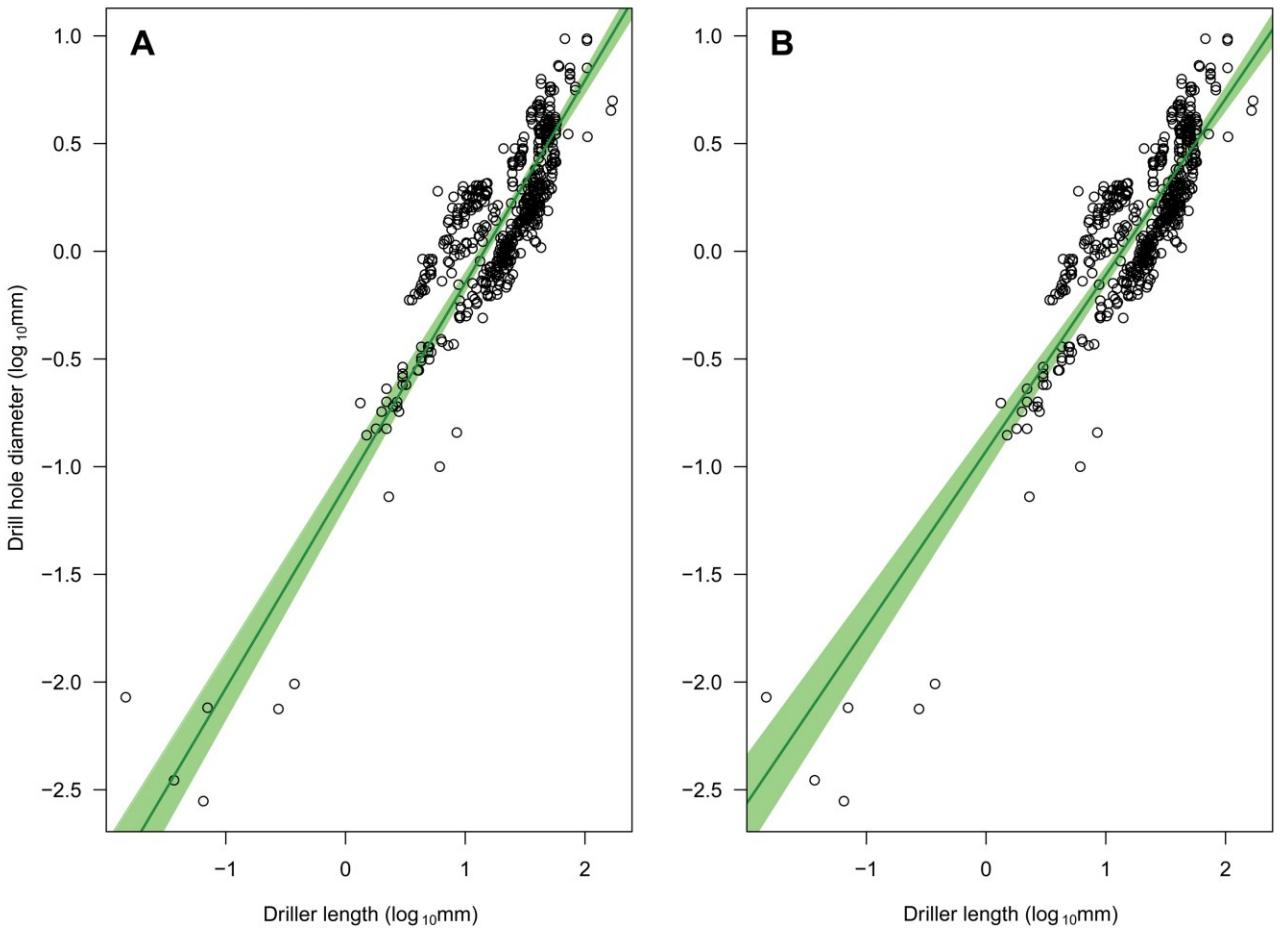

Figure S5. Log_{10}-scaled outer drill-hole diameter versus predator shell length for modern drilling clades using two methods of regression. (**A**) Reduced major axis regression line supplemented by 95% bootstrapped confidence intervals. Slope = 0.94; intercept = -1.09. Same as Figure 1. (**B**) Ordinary least squares axis regression line supplemented by 95% bootstrapped confidence intervals. Slope = 0.82; intercept = -0.93.

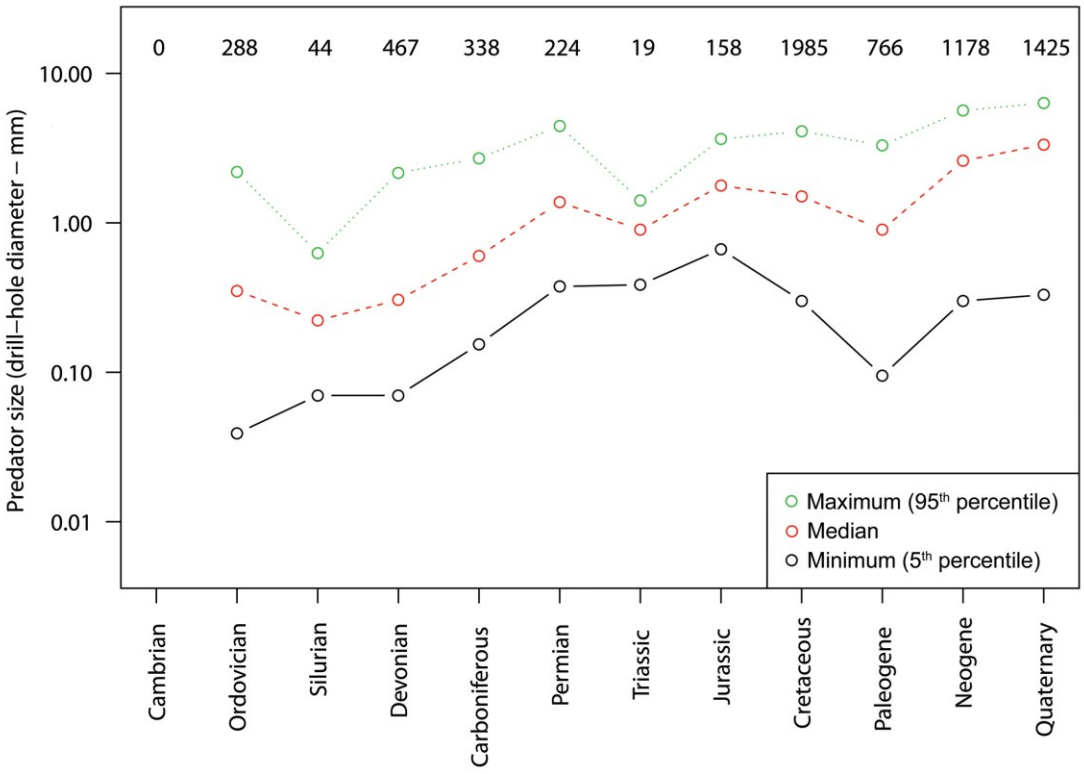

Figure S6. Minimum, median, and maximum drill-hole sizes through time. The maxima and minima are based on the true minimum and maximum values reported, and are not based on the minima and maxima of the medians within each bin as in Figure 2B. Numbers represent the number of specimens per bin. Percentiles are used to remove outliers (*48*).

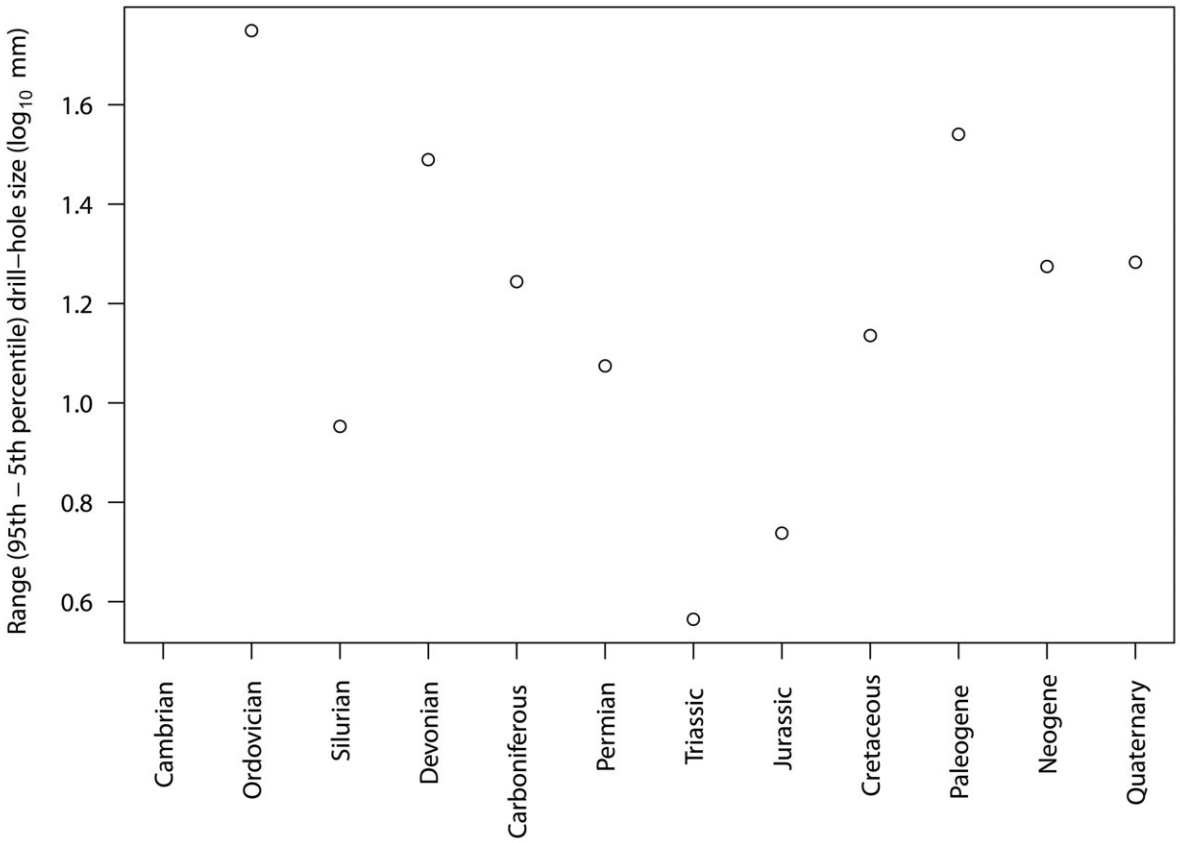

Figure S7. Differences between the 95th percentile of the maximum drill-hole sizes a nd the 5th percentile of the minimum drill-hole sizes through time. No significant tren d is apparent despite increasing sample sizes in the Cenozoic (Pearson's product-moment correlation p = 0.76, using numerical midpoints of periods).

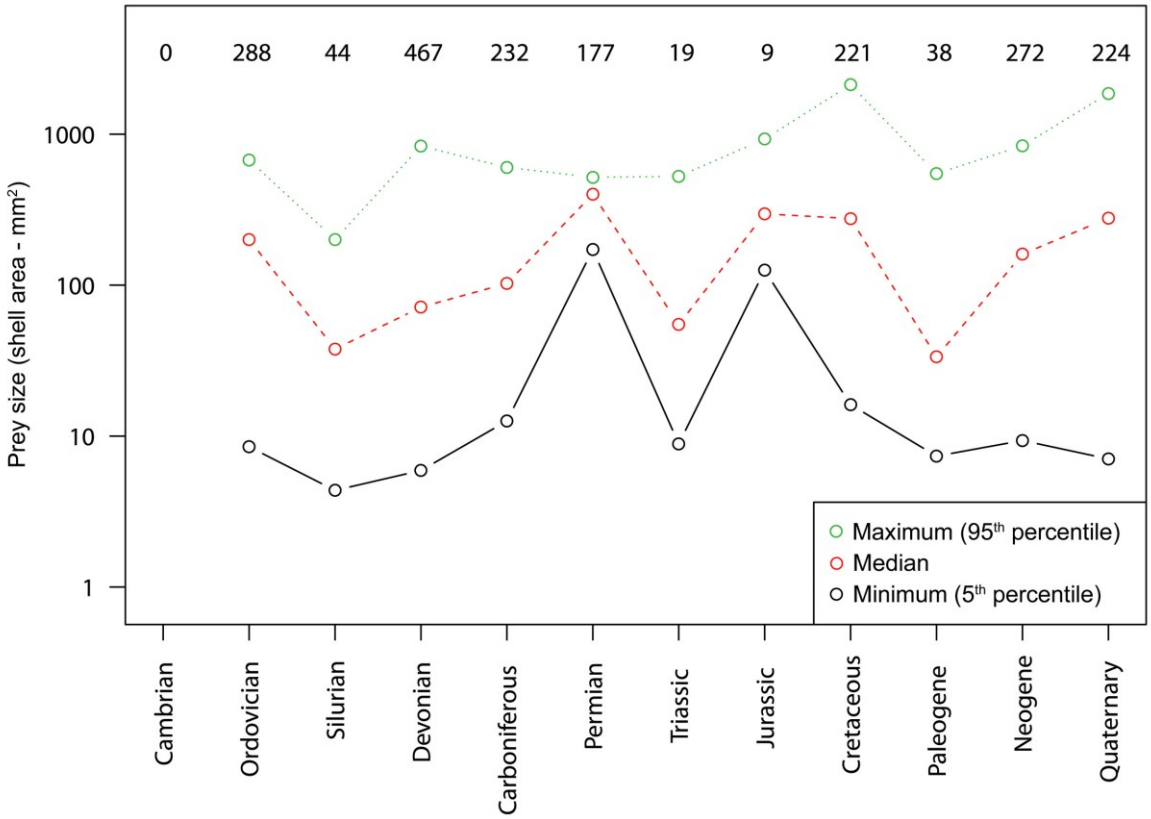

Figure S8. Minimum, median, and maximum prey shell sizes through time. The maxima and minima are based on the true minimum and maximum values reported, and are not based on the minima and maxima of the medians within each bin as in Figure 2A. Numbers represent the number of specimens per bin. Percentiles are used to remove outliers (*48*).

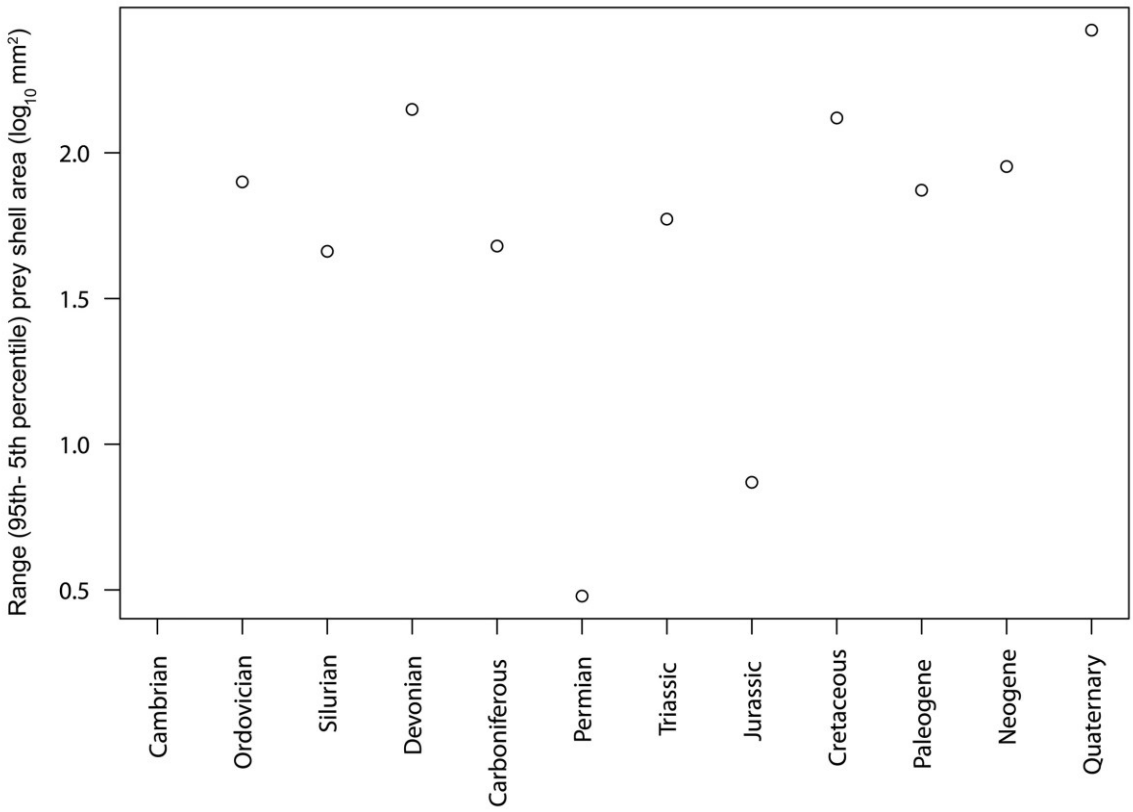

Figure S9. Differences between the 95th percentile of the maximum prey shell sizes a nd the 5th percentile of the minimum prey shell sizes through time. No significant tre nd is apparent despite increasing sample sizes in the Cenozoic (Pearson's product-momen t correlation p = 0.53, using numerical midpoints of periods).

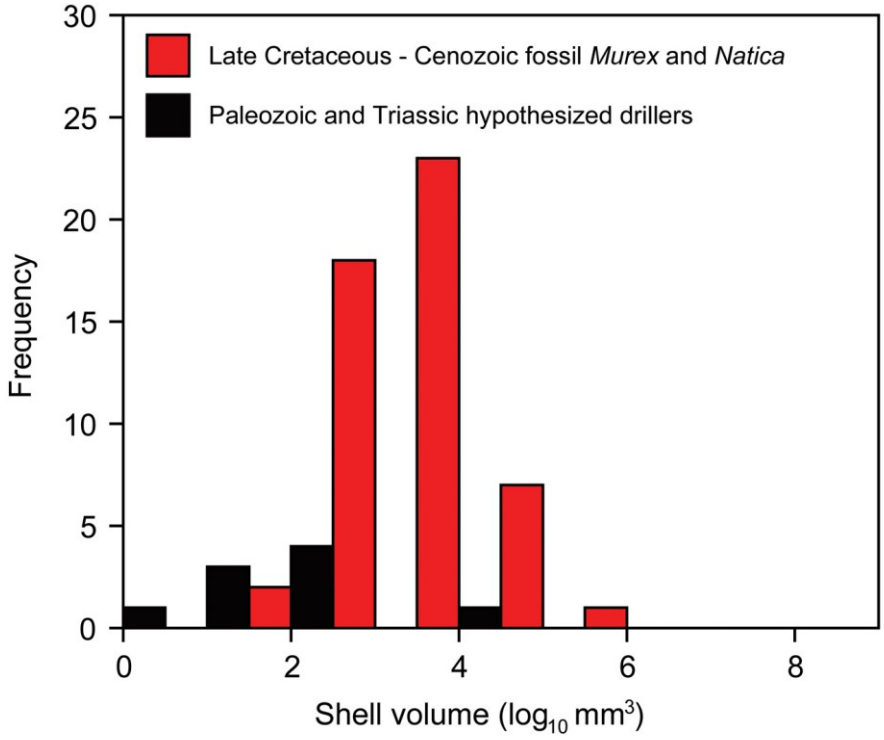

Fig. S10. Comparison of shell volumes from fossil drillers with modern representatives and older, hypothesized fossil drilling predators. Specifically, comparison is made between the volumes of the holotypes or largest syntypes of Late Cretaceous – Cenozoic fossil species of *Natica* and *Murex* versus those from hypothesized Paleozoic – Triassic predatory drillers. The latter taxa are statistically smaller (Mann-Whitney U = 101.5; p = 0.01). Data in Tables S20–S21.

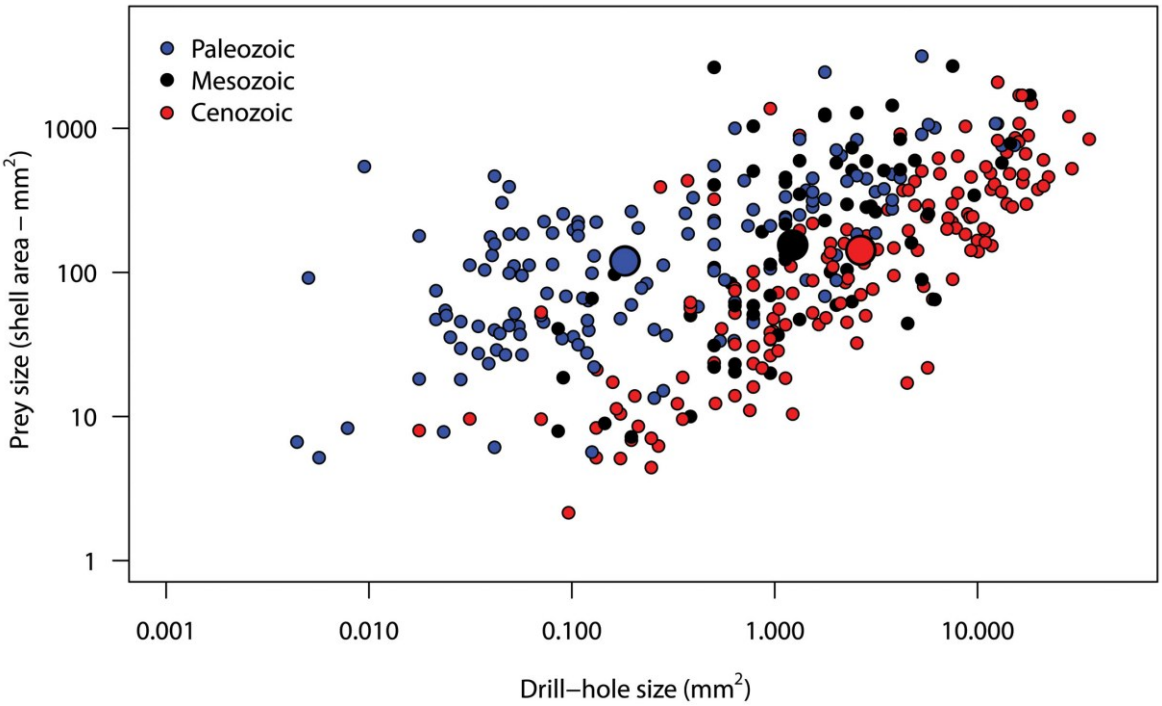

Figure S11. The relationship between prey shell area and drill-hole area color-coded by era. There is a shifting positive relationship between prey size and drill-hole size as predator size increases through time. Larger circles represent median centroids per era. Prey size remains relatively stable through time and does not appear to widen or narrow (compare the Cenozoic and Paleozoic).

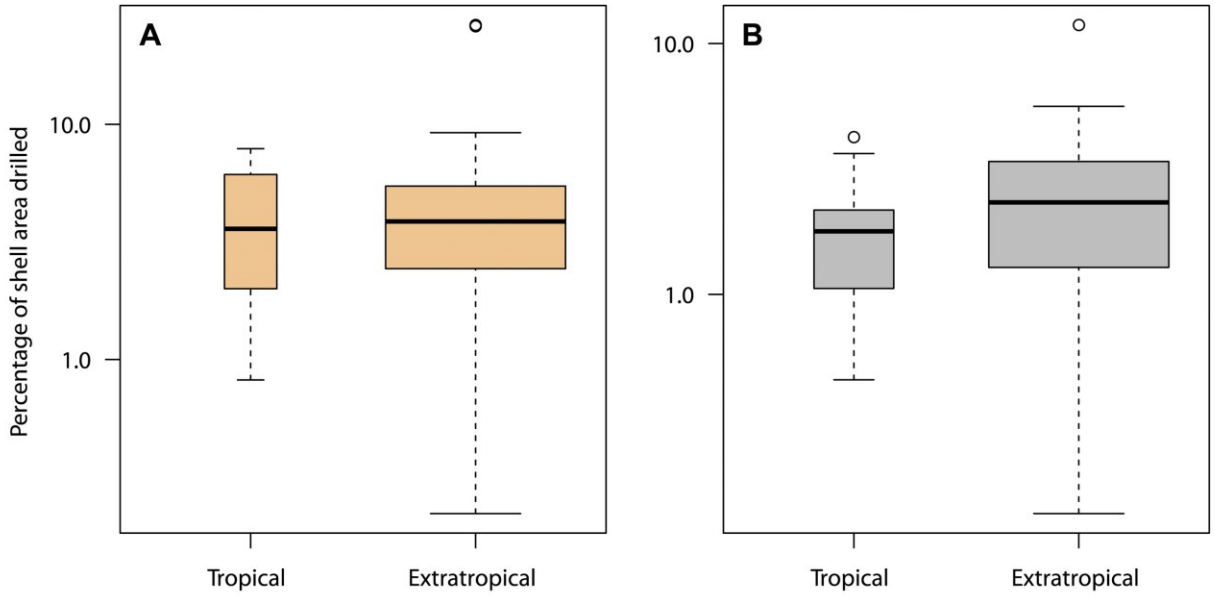

Fig. S12. No significant differences exist between the percentage of Cenozoic mollusks drilled as a proxy for predator-prey size ratios for tropical and extratropical regions (> 30°). (**A**) Gastropods; Wilcoxon W = 141, p = 0.88; sample sizes: 5 and 59, resp. (**B**) Bivalves; Wilcoxon W = 245, p = 0.29; sample sizes: 11 and 56, resp.

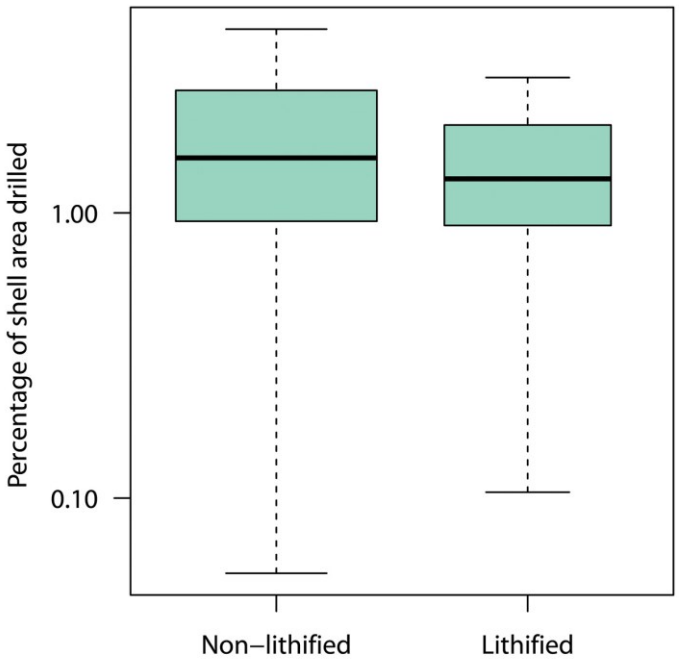

Fig. S13. No significant differences exist between the percentage of Cenozoic bivalve shells drilled as a proxy for predator-prey size ratios for non-lithified and lithified sediments. Wilcoxon W = 476, p = 0.39; sample sizes: 35 and 24, resp. Boxplot widths proportional to √n. Sample sizes were too low for gastropods. Lithification data based on primary literature search and data from the Paleobiology Database.

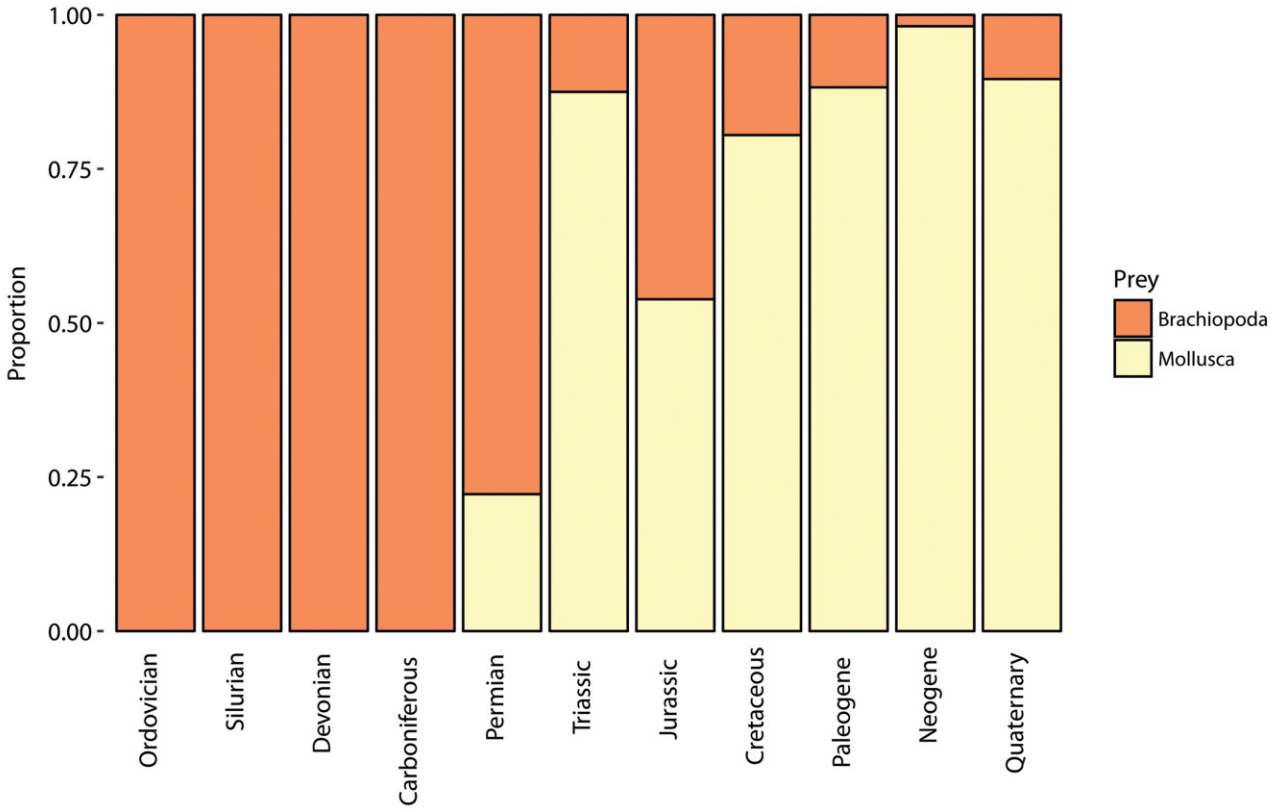

Fig. S14. Stacked bar chart showing the proportion of drilled brachiopod versus mollusk prey taxa for each Phanerozoic period. Sample sizes: Ordovician (20), Silurian (17), Devonian (49), Carboniferous (17), Permian (36), Triassic (16), Jurassic (13), Cretaceous (41), Paleogene (51), Neogene (54), Quaternary (49).

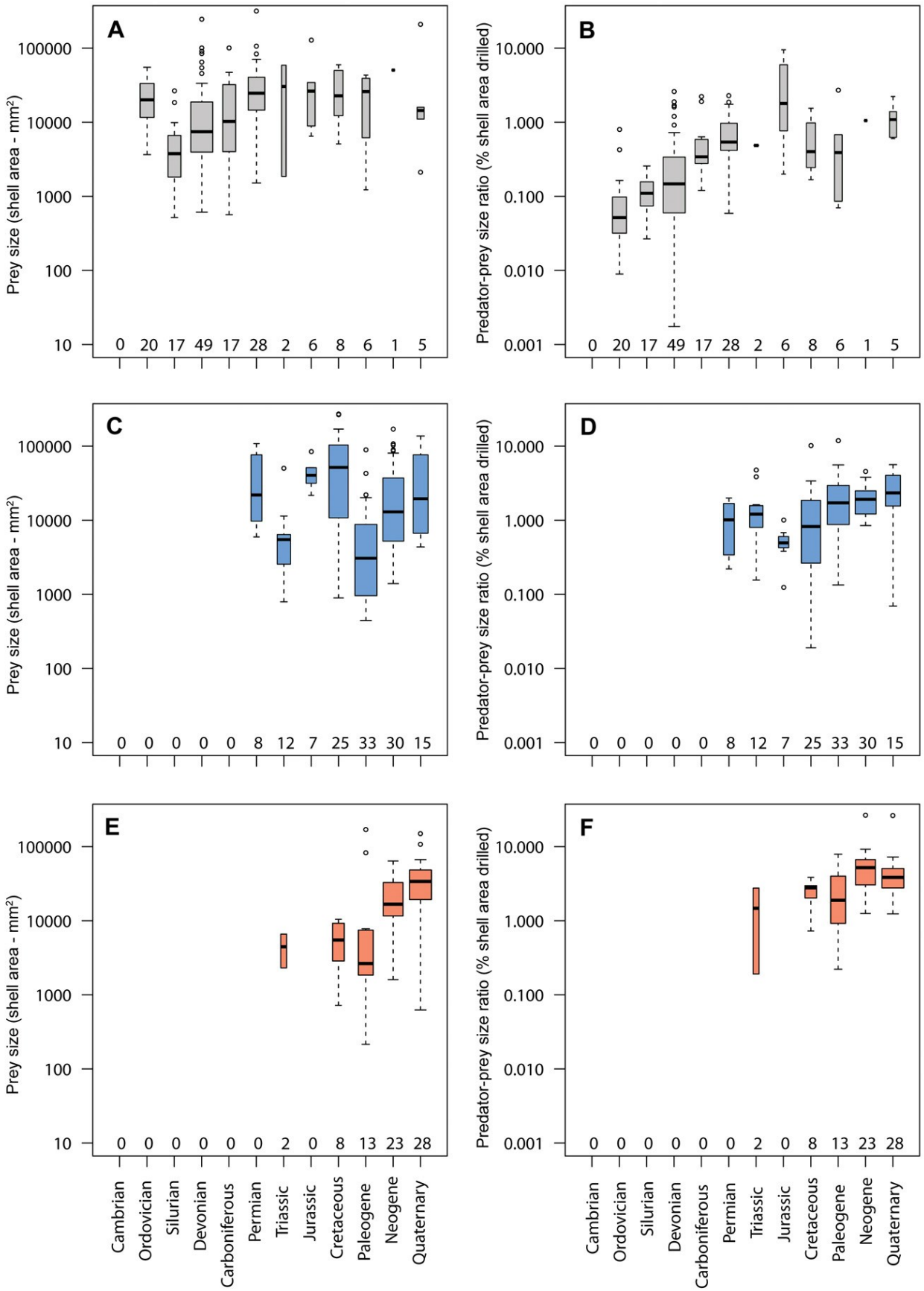
A
B
C
D
E
F
Prey size (shell area - mm²)
Predator-prey size ratio (% shell area drilled)
100000
10000
1000
100
10
10.000
1.000
0.100
0.010
0.001
0 20 17 49 17 28 2 6 8 6 1 5
0 0 0 0 0 8 12 7 25 33 30 15
0 0 0 0 0 0 2 0 8 13 23 28
Cambrian
Ordovician
Silurian
Devonian
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Neogene
Quaternary

Fig. S15. Shell areas (left) and the percentage of shell that is drilled (right) across the Phanerozoic. (**A, B**) Brachiopoda. (**C, D**) Bivalvia. (**E, F**) Gastropoda. Sample sizes indicated in lower part diagrams.

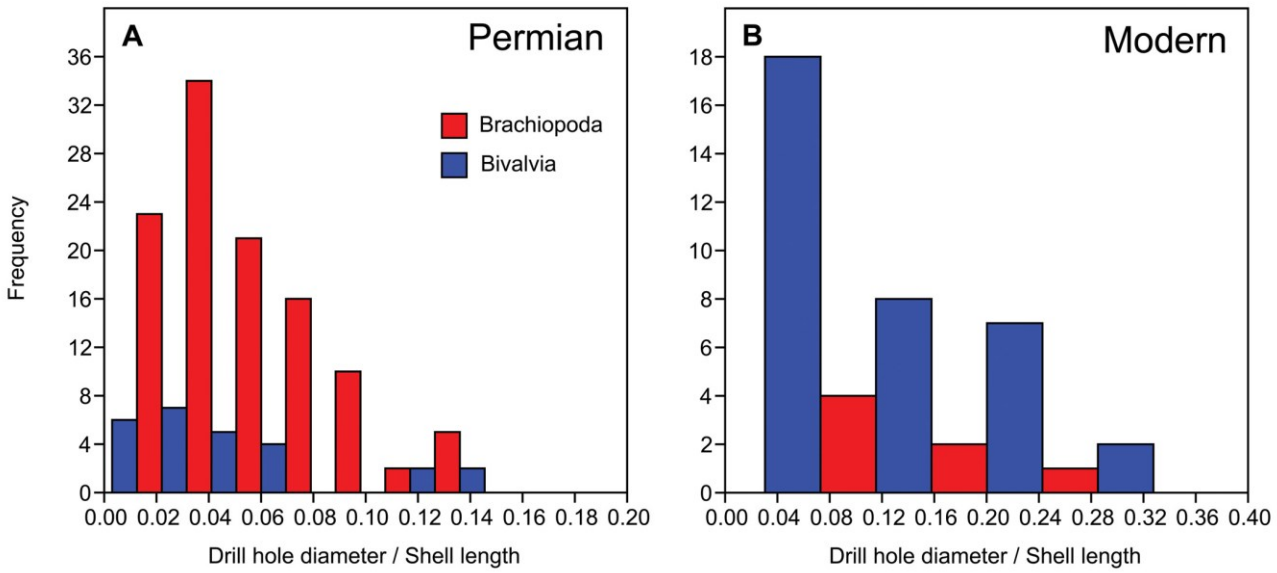

Fig. S16. Comparing the drill-hole diameter / shell lengths between brachiopod and bivalves for two assemblages. (**A**) Permian silicified brachiopods and bivalves from west Texas (USA) (data: (*29*)); Wilcoxon W = 1450, p = 0.97; brachiopod specimens: 111, bivalve specimens: 26. (**B**) A modern fauna from Brazil (data: (*30*)); Wilcoxon W = 142, p = 0.53; brachiopod specimens: 7, bivalve specimens: 35. The drill-hole diameter / shell lengths do not differ either between Permian bivalves and brachiopods mixed together from different geographic regions including Texas, Russia, Greece, and Brazil (Wilcoxon W = 95, p = 0.76; data: (*57*)). This result suggests that the lack of differences is not only found in local to regional assemblages, but may represent a global signal.

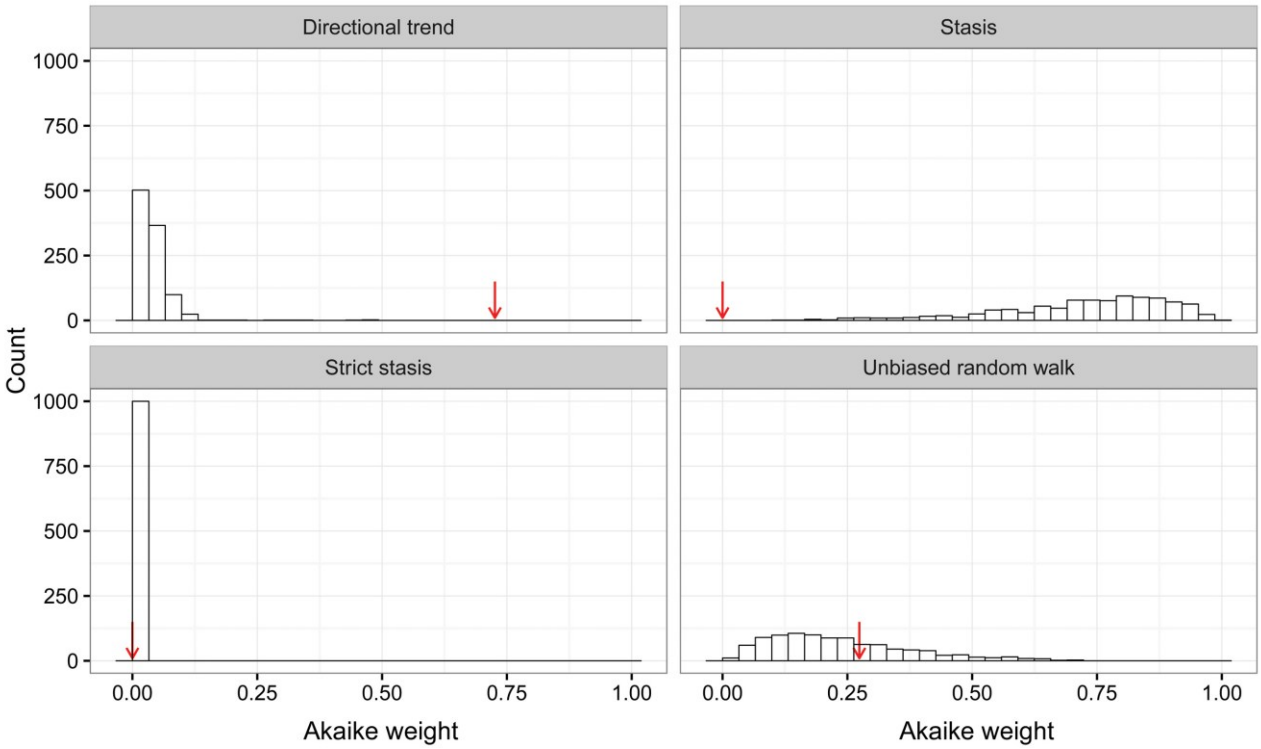

Fig. S17. Results of the permutation test simulating the expected trajectory of predator-prey size ratios if the sizes of drill holes did not change through time within clades (brachiopods, bivalves, and gastropods). Number of iterations = 1000. Most iterations were best fit by a stasis model (median AIC weight = 0.746), with some best fit by an unbiased random walk model (median AIC weight = 0.213). The median AIC weight for the directional trend model was 0.033, with a maximum of 0.505. The probability of generating the observed directional trend model AIC weight of 0.726 entirely through replacement among prey clades is thus < 0.001. The arrows indicate the support for each model using the true data (see Fig. 2C).

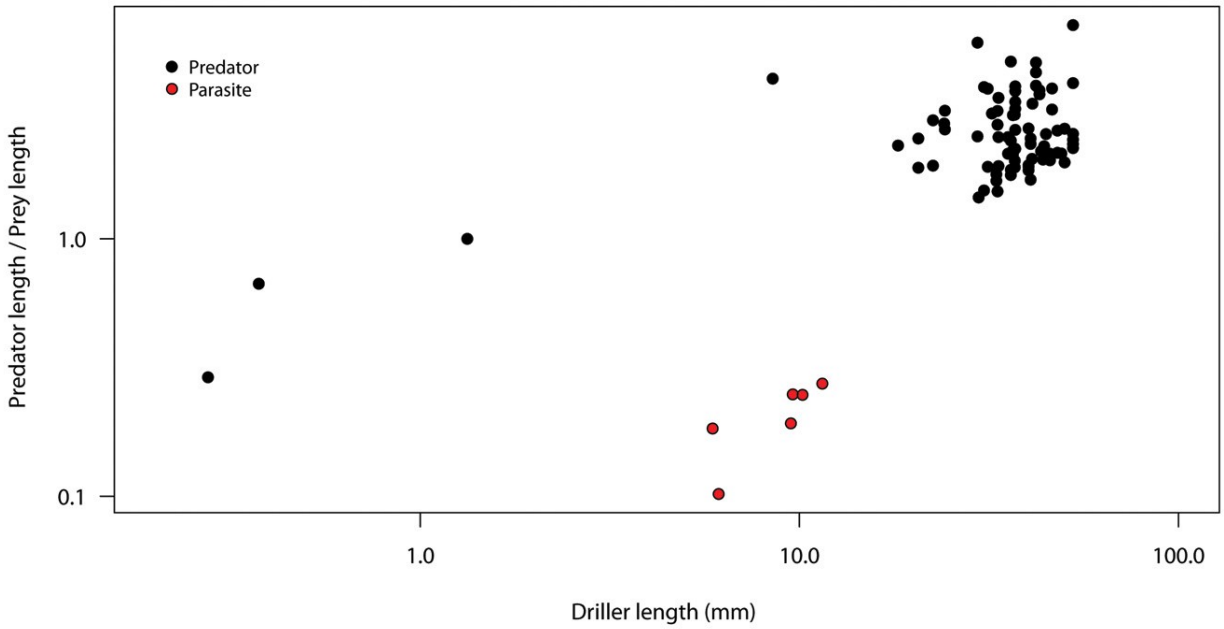

Fig. S18. Driller length/prey length versus driller length for modern drilling predators and parasites. Parasites tend to be smaller relative to their prey (driller length/prey length < 1) than predators are.

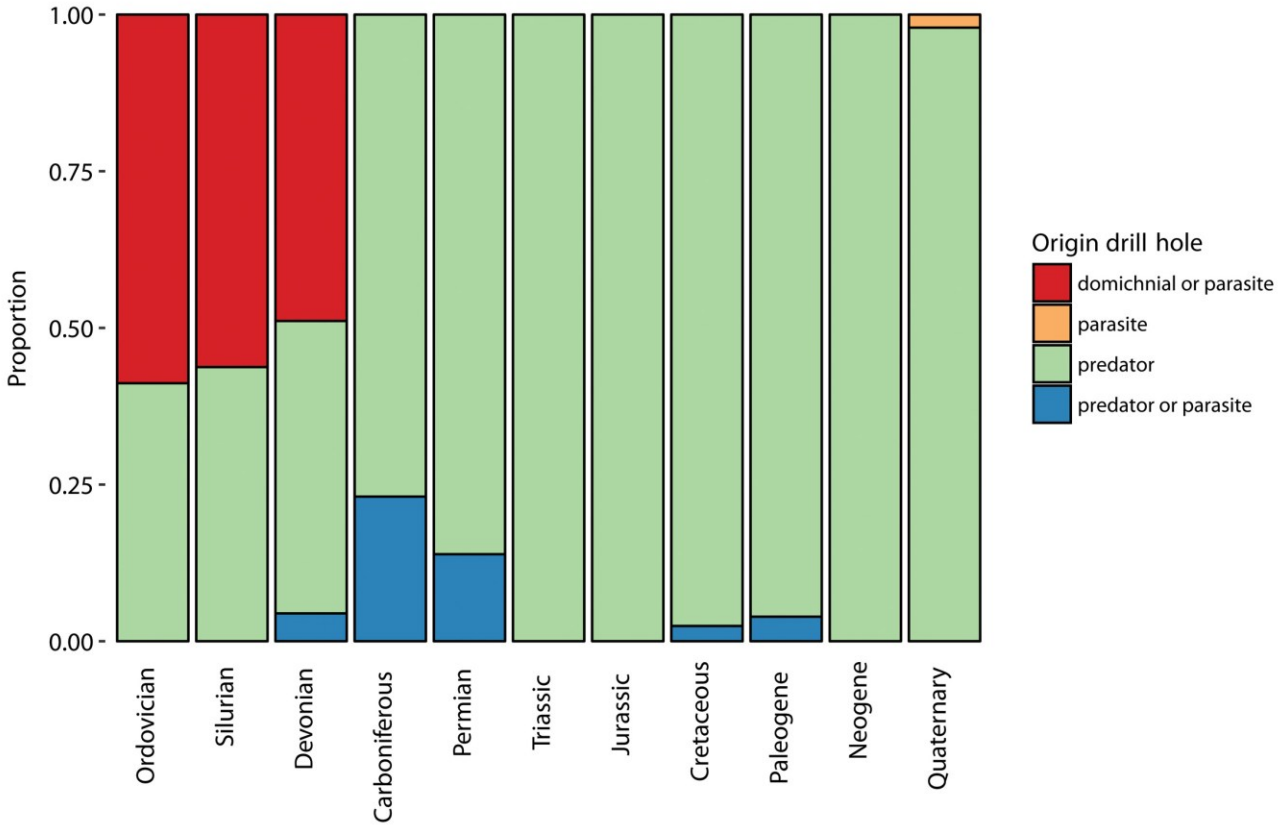

Fig. S19. Stacked bar chart showing the proportion of drill holes per category of inferred origin through the Phanerozoic. Sample sizes: Ordovician (17), Silurian (16), Devonian (45), Carboniferous (13), Permian (36), Triassic (16), Jurassic (11), Cretaceous (41), Paleogene (50), Neogene (54), Quaternary (49).

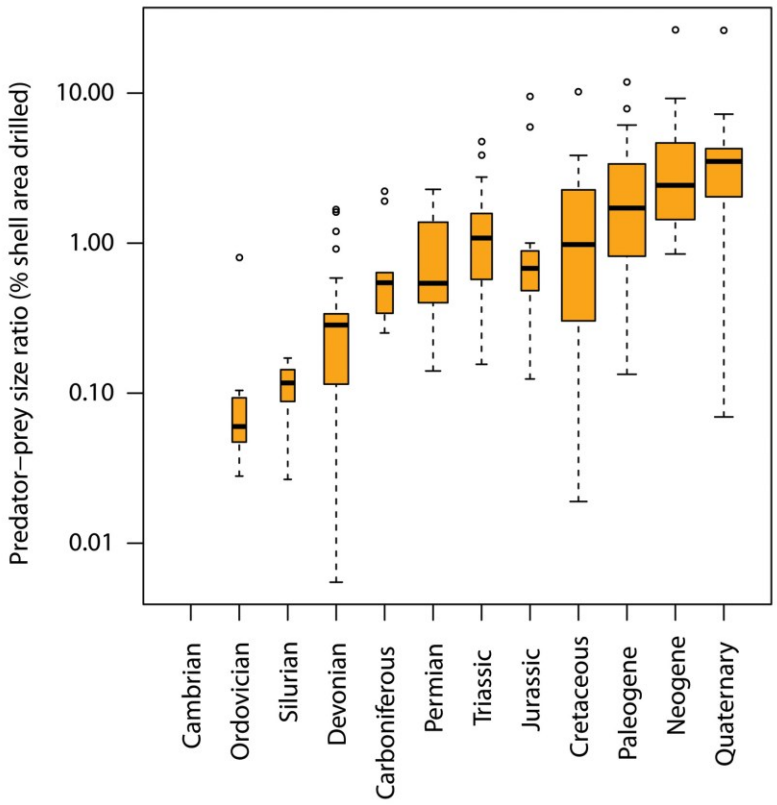

Fig. S20. Log_{10}-scaled boxplots of the percentage of shell drilled (proportional to predator-prey size ratio) in Phanerozoic brachiopods and mollusks using predatory drill holes only. Boxplot widths $\propto \sqrt{n}$; n per boxplot: 7–54. Table S14 shows support for each evolutionary model.

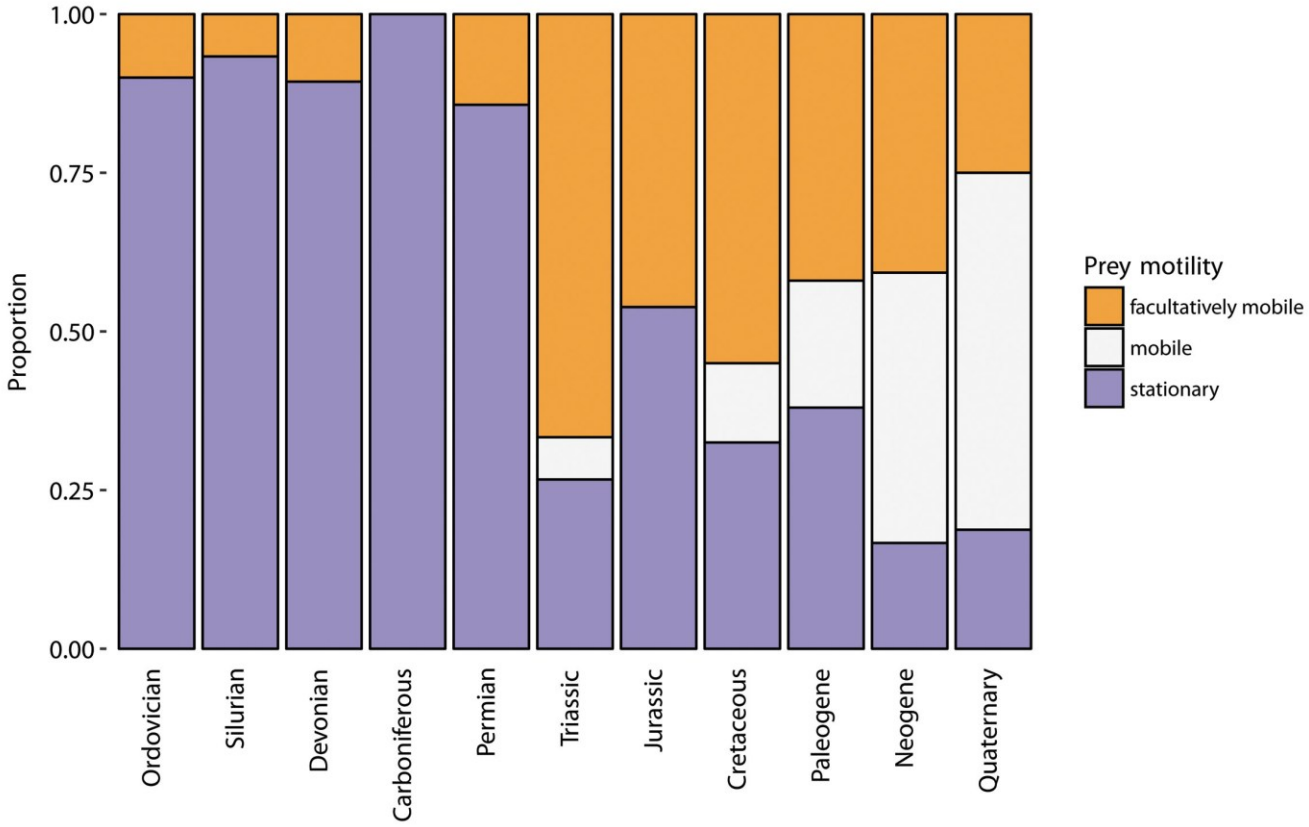

Fig. S21. Stacked bar chart showing the proportion of drill holes per category of prey motility through the Phanerozoic. Sample sizes: Ordovician (20), Silurian (15), Devonian (47), Carboniferous (17), Permian (35), Triassic (15), Jurassic (13), Cretaceous (40), Paleogene (50), Neogene (54), Quaternary (48).

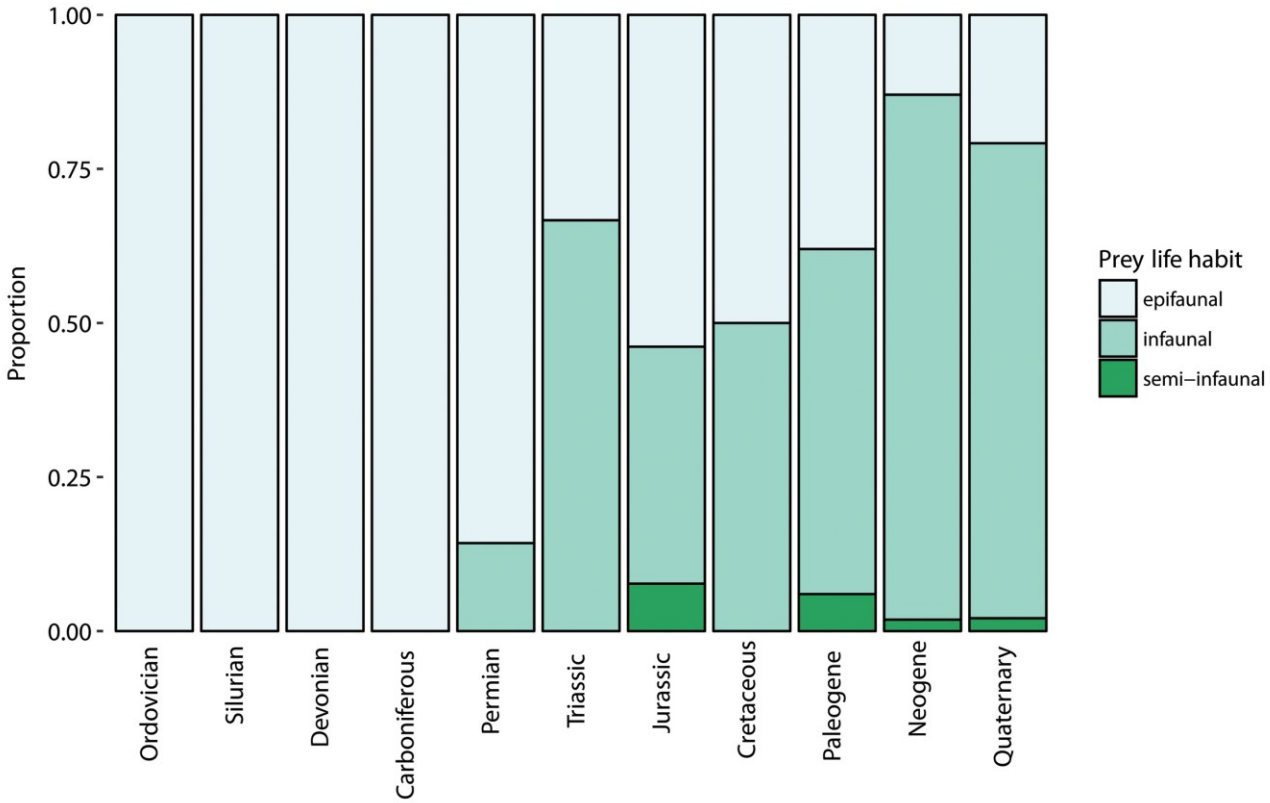

Fig. S22. Stacked bar chart showing the proportion of drill holes per category of life habit through the Phanerozoic. Sample sizes as in Figure S21. The increase in the frequency of drill holes among infaunal organisms starting in the early Mesozoic most likely reflects changes in abundance because occurrence data of marine invertebrates suggests a concurrent increase in the abundance of infaunal organisms (*19*, *78*).

Table S1. The life habits of marine and terrestrial drilling families for which drill-hole sizes and predator lengths are known. For full details, see External Database 1. Some other drillers are also known, but data on drill-hole sizes is lacking (see (*55*, *79*)).

Phylum of drillers	Class of drillers	Families containing drillers	Life habit drillers	Marine (M) or Terrestrial (T)	Reference(s), mainly those with size data
Mollusca	Gastropoda	Naticidae	Predatory, one omnivorous	M	(*62*, *80–82*)
Mollusca	Gastropoda	Muricidae	Predatory, some parasitic	M	(*63*, *65*, *83*, *84*)
Mollusca	Gastropoda	Cassidae	Predatory	M	(*69*, *85*)
Mollusca	Gastropoda	Okadaiidae	Predatory	M	(*86*)
Mollusca	Gastropoda	Nassariidae	Predatory	M	(*87*)
Mollusca	Gastropoda	Marginellidae	Predatory	M	(*88*)
Mollusca	Gastropoda	Eulimidae	Parasitic	M	(*89*, *90*)
Mollusca	Gastropoda	Capulidae	Parasitic	M	(*16*, *91*)
Mollusca	Gastropoda	Platyceratidae (fossil only)	Parasitic	M	(*58*, *76*, *77*)
Mollusca	Gastropoda	Oleacinidae	Predatory	T	(*92*)
Nematoda			Predatory	M	(*93*)
Foraminifera	Globothalamea	Turrilinidae	Predatory	M	(*94*)
Cercozoa		Viridiraptoridae	Predator or scavenging	T	(*95*)
Cercozoa		Vampyrellidae	Predatory	T	(*96*, *97*)
Arthropoda	Insecta	Drilidae	Predatory	T	(*98*)

Table S2. Results of evolutionary model comparisons for the size of Phanerozoic mollusk and brachiopod prey. Lower scores for the Akaike information criterion and higher Akaike weights indicate stronger support for the respective model. For the data used here see External Database 2.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	-6.22	3	21.87	0.005
Unbiased random walk	-6.22	2	17.95	0.036
Stasis	-2.93	2	11.36	0.959
Strict stasis	-39.99	1	82.42	0

Table S3. Results of evolutionary model comparisons for drill-hole diameters in Phanerozoic mollusk and brachiopod prey.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	1.34	3	6.75	0.177
Unbiased random walk	0.90	2	3.70	0.814
Stasis	-3.59	2	12.69	0.009
Strict stasis	-257.12	1	516.68	0

Table S4. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	5.02	3	-0.60	0.726
Unbiased random walk	2.08	2	1.34	0.274
Stasis	-8.65	2	22.80	0
Strict stasis	-316.03	1	634.50	0

Table S5. Results of evolutionary model comparisons for drill-hole diameter / prey length for Phanerozoic mollusks and brachiopods.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	12.17	3	-14.92	0.624
Unbiased random walk	9.70	2	-13.91	0.376
Stasis	0.03	2	5.44	0
Strict stasis	-237.94	1	478.33	0

Table S6. Results of evolutionary model comparisons for drill-hole diameter / prey width for Phanerozoic mollusks and brachiopods.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	12.13	3	-14.83	0.747
Unbiased random walk	9.08	2	-12.67	0.253
Stasis	-2.07	2	9.63	0
Strict stasis	-340.80	1	684.04	0

Table S7. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic gastropods and brachiopods.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	1.64	3	6.14	0.616
Unbiased random walk	-0.79	2	7.08	0.384
Stasis	-9.60	2	24.69	0
Strict stasis	-311.80	1	626.03	0

Table S8. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic bivalves and brachiopods.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	4.20	3	1.03	0.592
Unbiased random walk	1.86	2	1.78	0.408
Stasis	-7.62	2	20.75	0
Strict stasis	-248.54	1	499.53	0

Table S9. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for North American, Phanerozoic mollusks and brachiopods.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	3.43	3	3.94	0.518
Unbiased random walk	0.96	2	4.08	0.482
Stasis	-8.05	2	22.09	0
Strict stasis	-258.82	1	520.20	0

Table S10. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods using the median and squared standard error as inputs for the model instead of the mean and variance (see (*53*)**).**

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	3.44	3	2.54	0.746
Unbiased random walk	0.40	2	4.70	0.254
Stasis	-9.08	2	23.67	0
Strict stasis	-329.15	1	660.75	0

Table S11. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods using the mid-point of periods instead of the age of the median data point.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	5.91	3	-2.38	0.893
Unbiased random walk	1.82	2	1.85	0.107
Stasis	-8.65	2	22.80	0
Strict stasis	-316.03	1	634.50	0

Table S12. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods with lengths or widths > 5.0 mm.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	5.27	3	-1.12	0.738
Unbiased random walk	2.27	2	0.95	0.262
Stasis	-8.41	2	22.33	0
Strict stasis	-286.83	1	576.10	0

Table S13. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods without size restrictions (including shells < 2 mm in size).

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	5.00	3	-0.57	0.723
Unbiased random walk	2.08	2	1.35	0.277
Stasis	-8.65	2	22.79	0
Strict stasis	-316.65	1	635.75	0

Table S14. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods using inferred predatory drill holes only.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	3.39	3	2.66	0.594
Unbiased random walk	1.04	2	3.42	0.406
Stasis	-7.79	2	21.09	0
Strict stasis	-147.00	1	296.45	0

Table S15. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods using a minimum sample size per data point of two instead of one.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	3.48	3	2.47	0.649
Unbiased random walk	0.90	2	3.70	0.351
Stasis	-9.11	2	23.72	0
Strict stasis	-261.24	1	524.92	0

Table S16. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods using stationary prey only.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	3.36	3	2.70	0.609
Unbiased random walk	0.96	2	3.59	0.391
Stasis	-7.10	2	19.70	0
Strict stasis	-109.78	1	222.00	0

Table S17. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods using epifaunal prey only.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	3.01	3	3.40	0.555
Unbiased random walk	0.83	2	3.85	0.444
Stasis	-7.06	2	19.63	0
Strict stasis	-98.48	1	199.39	0

Table S18. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) by approximating shell area for gastropods as a cone and doubling valve area for bivalves and brachiopods.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	5.34	3	-1.25	0.698
Unbiased random walk	2.54	2	0.42	0.302
Stasis	-8.03	2	21.57	0
Strict stasis	-301.57	1	605.59	0

Table S19. Results of evolutionary model comparisons for the proportion of shell drilled (drill-hole area / shell area) by approximating shell area for gastropods as a cone and bivalves and brachiopods as an ellipsoid.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Directional trend	5.28	3	-1.14	0.671
Unbiased random walk	2.60	2	0.29	0.329
Stasis	-7.71	2	20.91	0
Strict stasis	-285.34	1	573.13	0

Table S20. Results of evolutionary model comparisons including complex models for the proportion of shell drilled (drill-hole area / shell area) for Phanerozoic mollusks and brachiopods. Cenozoic periods are subdivided into epochs.

	Log likelihood	Free parameters	Akaike information criterion (AICc)	Akaike weight
Strict stasis	-322.44	1	647.19	0
Stasis	-11.54	2	28.08	0
Unbiased random walk	1.37	2	2.25	0.292
Directional trend	3.84	3	0.50	0.699
Punctuation	-5.02	4	22.03	0
Stasis-Unbiased random walk	-4.29	4	20.58	0
Stasis-Directional trend	0.30	5	16.07	0
Unbiased random walk-Stasis	3.63	5	9.41	0.008
Directional trend-Stasis	4.72	6	13.06	0.001

Table S21. Sizes of late Phanerozoic drillers. Sizes collected from the primary literature of the holotypes or largest syntypes of late Phanerozoic (Late Cretaceous – Cenozoic) fossil species of the type genera of the two best-known and extant predatory drilling families, *Natica* of the Naticidae and *Murex* of the Muricidae, as listed in the Paleobiology Database (11/01/2016).

	Height (mm)	Width (mm)	Shell volume (mm^3)	log_{10}(Shell volume)
Murex asteriscus Tate, 1888	27	19	2550.47	3.41
Murex bifrons Tate, 1888	15.5	6	146.01	2.16
Murex calvus Tate, 1888	22	9	466.29	2.67
Murex camplytropis Tate, 1888	16	9	339.12	2.53
Murex crowfootii Wood, 1879	incomplete			
Murex didymus Tate, 1888	17.5	6.5	193.47	2.29
Murex fluctuosus Forbes, 1846	31.8	40.2	13447.07	4.13
Murex grooti Jenkins, 1864	45.5	31.8	12039.65	4.08
Murex hamiltonensis Tate, 1888	20	9	423.90	2.63
Murex junghuhni Martin, 1879	62	41	27271.42	4.44
Murex macgillivrayi Dohrn, 1862	60	20		
Murex manubriatus Tate, 1888	24	8	6280.00	3.80
Murex minutus Johnston, 1879	8.5	4.5	401.92	2.60
Murex mississippiensis Conrad, 1848	43.2		45.04	1.65
Murex pachystirus Tate, 1888	24	15.5		
Murex paradoxicus Jenkins, 1864	30.7	20.1	1508.77	3.18
Murex pondicherriensis Forbes, 1846	25.4	19.1	3245.48	3.51
Murex pseudonystii Wood, 1879	28.6	19.1	2424.65	3.38
Murex reedi Wood, 1877	41.3	22.2	2730.12	3.44
Murex rhysus Tate, 1888	32	14	5326.04	3.73
Murex sandersoni Cox, 1930	45	31	1641.17	3.22
Murex scorpionius Olsson, 1930	16.5	8.25	11315.78	4.05
Murex torturosus Sowerby, 1823	42	19.5	293.86	2.47
Murex trinchinopolitensis Forbes, 1846	33	17.8	4178.95	3.62
Murex trinodosus Tate, 1888	20	8.5	2735.91	3.44
Murex wadiai Cox, 1930	31	18	378.11	2.58
Natica alazana Cooke, 1928	6	5	39.25	1.59
Natica bandongensis Martin, 1879 (largest syntype)	41	36.5	14292.82	4.16
Natica bolus Brown and Pilsbry, 1913	9	9.5	212.54	2.33
Natica bulbulus White, 1887		10		
Natica callosior Martin, 1879	32.5	28.5	6907.51	3.84
Natica canalizonalis Brown and Pilsbry, 1913	8	8.3	144.21	2.16
Natica clarki Etherington, 1931	17.2	16.1	1166.62	3.07
Natica cliftonensis Clark, 1895	10	12	376.80	2.58

Natica conradiana Gabb, 1864	35.3	39.5	14411.77	4.16
Natica coxi Mukerjee, 1939	16.4	12.3	649.24	2.81
Natica dorothiensis Stephenson, 1953	18.3	15	1077.41	3.03
Natica eminulopsis Maury, 1912	12	9	254.34	2.41
Natica engenholyria Maury, 1936		55		
Natica epiglottina Lamarck, 1804	20	13	884.43	2.95
Natica eurydice White, 1887		40		
Natica exilis Bohm, 1926	not found			
Natica farafrensis Wanner in Oppenheim, 1902	8			
Natica globosa Philippi, 1855	not found			
Natica hugardiana d'Orbigny, 1842	70	75	103031.25	5.01
Natica mississippiensis Conrad, 1848	20.3			
Natica morraboolensis Tate, 1893	28	27.5	5540.79	3.74
Natica neptuni d'Orbigny, 1850				
Natica obliquistriata Forbes, 1846	25.4	20.3	2738.89	3.44
Natica obscura Sowerby, 1840	not found			
Natica pagoda Forbes, 1846	38.1	19.1	3636.97	3.56
Natica parahybensis Maury, 1930		70		
Natica paytensis Olsson, 1930	11	12	414.48	2.62
Natica permunda Conrad, 1854	18.7	18.2	1620.81	3.21
Natica rostalina Jenkins, 1864	24.3	22.2	3133.72	3.50
Natica rugosissima Forbes, 1846	14.8	8.5	279.80	2.45
Natica stoddardi Hislop, 1859	35.6	28	7303.22	3.86
Natica striolata Sowerby, 1846	no measurements given			
Natica subvarians Tate, 1893	24	17	1814.92	3.26
Natica sulcatula Bose, 1906	11	9	233.15	2.37
Natica suturalis Forbes, 1846	15.2	12.7	641.50	2.81
Natica varians Tate, 1893	40	32	10717.87	4.03
Natica vokesi Addicott, 1966	20.1	19.4	1979.47	3.30
Natica youngi Maury, 1917 (largest syntype)	23	22	2912.87	3.46

Table S22. Sizes of hypothesized early Phanerozoic drillers. Specifically, sizes are given for Paleozoic – Triassic predatory drilling taxa suggested in the literature excluding parasitic species found attached to echinoderms. All species listed here are gastropods.

	Height (mm)	Width (mm)	Shell volume (mm^3)	log_{10}(Shell volume)	Referral to taxon as possible driller
Pseudorthonychia alata (Laube, 1869)	4	3	9.42	0.97	(*56*)
Ptychostoma sanctaecrucis (Wissman in zu Münster, 1841)	15	13	663.33	2.82	(*99*)
Prostylifer paludinaris (zu Münster, 1841) (= *Amauropsis subhybrida* (d'Orbigny, 1849))	8.5	5.9	77.42	1.89	(*99*)
Lophospira perlamellosa Ulrich, 1897	13	10	340.17	2.53	(*100*)
Glyptotomaria genundewa Clarke, 1904	4.7	5	30.75	1.49	(*101*)
Glyptotomaria ciliata Clarke, 1904	7.6	7.5	111.86	2.05	(*101*)
Platyostoma perceense (Clarke, 1908)	60	58	52814.80	4.72	(*102*)
Naticonema kauffmani Peel, 1975	7.2	6.3	74.78	1.87	(*101*, *103*)
Naticonema similare Perner, 1903	10.8	13.1	484.97	2.69	(*101*, *103*)

Not included:	
"Naticonema" lineatum (Conrad, 1842) found as parasite on crinoid (*104*)	(*101*, *103*, *105*)
"Naticonema" niagarense (Hall, 1852) found as parasite on crinoid (*106*)	(*101*, *103*)
Platyceras spirale Hall, 1859, found as parasite on crinoid (*107*)	(*102*)
Platyceras bucculentum Hall, 1862, found as parasite on crinoid (*108*)	(*109*), cooccurrence
Platyceras rarispinum Hall, 1859, found as parasite on crinoid (*108*)	(*109*), cooccurrence

External Database 1. Data used for drill-hole size and predator size analyses of primarily extant drilling taxa.

External Database 2. Data used for Phanerozoic drill-hole size and prey size analyses.

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