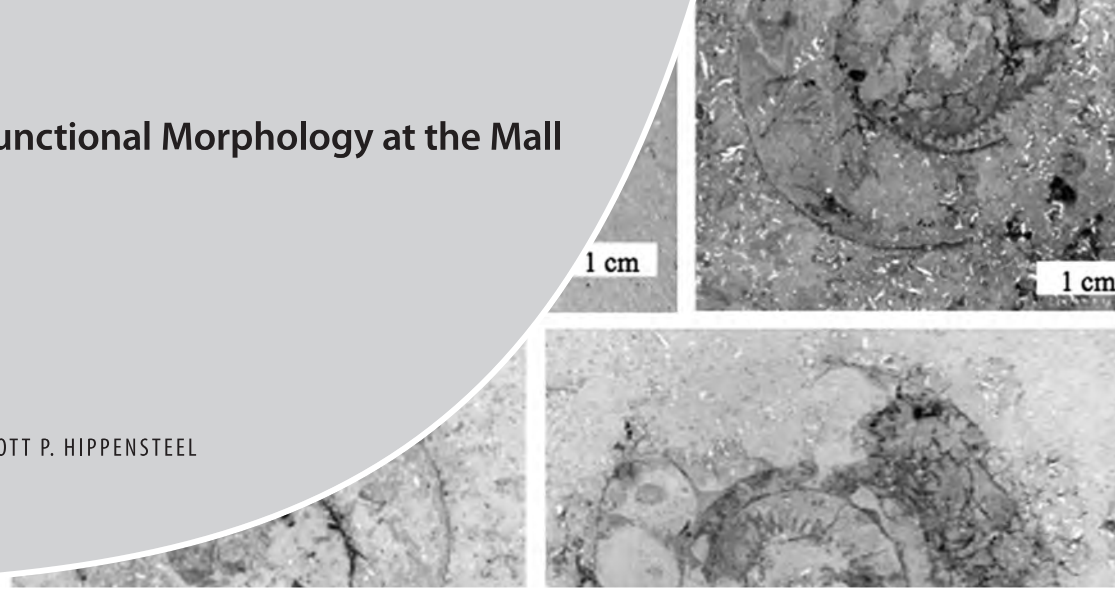
RESEARCH ON LEARNING

Functional Morphology at the Mall



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Abstract

The primary decorative flooring tile in the Southpark Mall in Charlotte, North Carolina, is fossiliferous limestone that contains Jurassic ammonoids and belemnoids. Visible in these tiles are more than 500 ammonoids, many of which have been cross sectioned equatorially perpendicular to the plane of coiling. Upper-level undergraduate students from UNC Charlotte used this data set to measure ammonoid coiling geometry and, thus, coiling strategy, and their findings were compared with earlier reported research presented in highly respected paleobiology journals. This example of urban paleobiology utilized a large, easily accessible, and readily available fossil data set to introduce functional morphology of coiled cephalopods. Similar data sets are available in public buildings around the United States, providing a valuable fossil resource at a time when shrinking academic budgets would prohibit purchasing such a collection (and many collections have not been updated in decades). As students compared their results with those previously published by professional paleontologists, they were exposed to the methods and limits of the scientific method in the historical sciences, as well as the dangers of poor sample selection.

Key Words: *Ammonoids; function morphology; restricted geometry.*

University faculty, and especially those who teach undergraduates in urban settings, have shown an increased interest in incorporating urban geoscience topics in their classes (Horenstein, 2008). These curricular issues range from building-stone geology, to cemetery gravestones, to the analysis of sidewalk fractures (Fazio & Nye, 1980). Additionally, examples of urban field trips exist for numerous cities (e.g., Fazio, 1981).

Although examples of urban geology in the undergraduate curricula are numerous, those of urban paleobiology are less frequent. This paper presents an example of how a common type of decorative building stone, fossiliferous limestone enriched with coiled cephalopods, can be used to teach the concept of functional morphology. Fossiliferous limestone is a common building material. Mississippian Salem Limestone or "Indiana Limestone," for example, is especially common and is used as a decorative stone in famous buildings such as the Lincoln Memorial and Reflecting Pool in Washington, D.C. The monuments and museum buildings in the nation's capital are highly enriched with fossils, and Web-based guides exist that describe fossiliferous decorative stones used in the architecture (http://www.dcfossils.org). Similar limestones are found in buildings from across the United States, including the State Capital Buildings in Richmond, Virginia; Raleigh, North Carolina; and Columbus, Ohio; as well as the Orlando International Airport and the Minneapolis–St. Paul International Airport.

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○ The Fossiliferous Limestone of Southpark Mall, Charlotte, North Carolina

Southpark was constructed in 1970 and contains more than 160 stores. The majority of the floor of the ~1.5 million feet^2 shopping complex is covered with 45 × 45 cm tiles composed of two varieties of fossiliferous limestone. The primary decorative stone, ~80% by surface area, is a light beige limestone that contains abundant ammonoids and belemnoids (Figure 1). The other 20% of the flooring is a darker blue-gray limestone that also contains ammonoids and belemnoids. These two varieties of limestone provide two different data sets for measuring the cross sections of the ammonoids and may represent rock taken from different quarries, depositional localities, or periods.

The current owners of the property, Simon Property Group, did not have records of the source of the stone used for the tile floor but provided contact information for the architects of the building project. Richard Bartlett of Bartlett, Hartley and Mulkey Architects PA described the tile as "Jura Stone Light Beige

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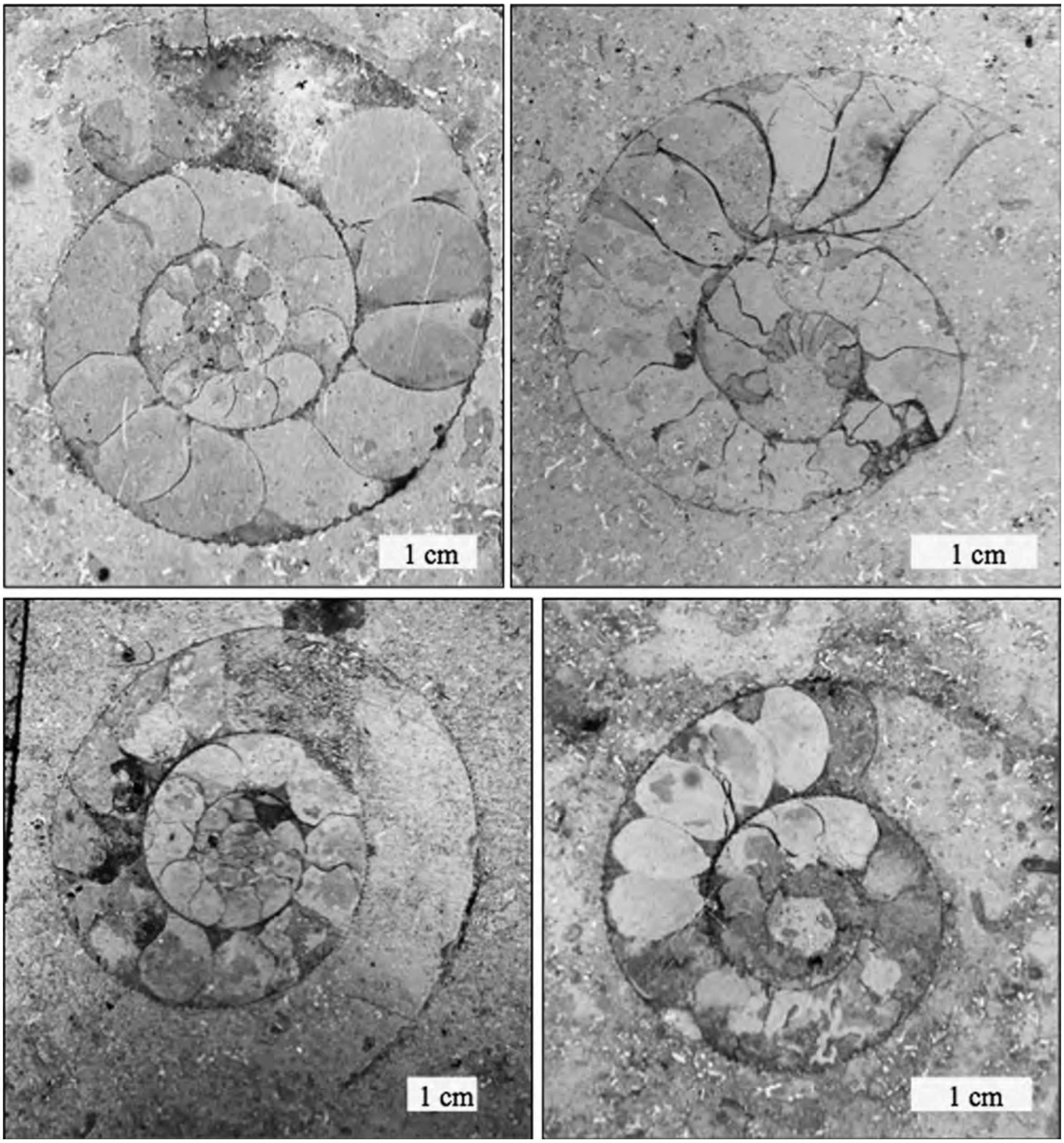

Figure 1. Ammonoid cross sections in the tile from Southpark Mall, Charlotte, North Carolina.

(light tan) and Jura Stone Blue-gray," both of which originated in Germany. He also helpfully provided the contact information for the installer of the tile, George Combis, who, in turn, contacted his tile supplier in Italy. Although the Italian supplier could not definitely document the 40-year-old tile's source, the limestones were both likely quarried from the Franconian Region of southern Germany (just north of Bavaria). If so, they were deposited ~160 million years ago, during the Upper Malm Epoch (Late Jurassic Period).

The surveys in the present study indicate that more than 800 ammonoids and 300 belemnoids are present in the tile of the shopping complex. Approximately half of these ammonoids are sectioned in a manner that allows for measurement of their internal geometry across the axis of coiling. It is fortunate that this floor was covered in limestone and not the marble that is present as a façade in other portions of the shopping complex, because the metamorphism associated with the marble might have skewed the measurements of the ammonoid shell geometry or destroyed the fossils entirely.

○ Previous Studies of Functional Morphology

Balsam and Vogel (1973) and Savarese (1992) constructed mechanical models for archaeocyathids (cylindrical filter feeders) to test the flow of water currents through the organism and evaluate hydrodynamic efficiency. Stanley (1970, 1975) carried the use of mechanical models further when he compared the morphology of bivalves with their burrowing rate. In both examples, the geometry of the fossil was an important component of the tested hypothesis. Ammonoid shell streamlining was studied by Kummel and Lloyd (1955) using a circulating water channel and plaster models of ammonoid shells. All these studies are included in undergraduate paleobiology curricula and textbooks (e.g., Stearn & Carroll, 1989; Prothero, 1998), but students may gain a better understanding of functional morphology by reading the appropriate scientific literature and studying and measuring the fossils directly. One of the underlying goals of the present study was to give undergraduate students hands-on experimental involvement by having them compare their research and findings with the important earlier work on the coiling of ammonoids presented by David Raup (1967) in *The Journal of Paleontology*.

○ Restricted Geometry of Ammonoids

Cephalopods are perhaps the most common predator in the fossil record, and they are represented today by octopuses and squids. Only one living member has a hard external shell, the chambered nautilus. During the Devonian Period, the ammonoid cephalopods radiated and diversified and they survived repeated episodes of mass extinction followed by rapid diversification. None, however, survived the Late Cretaceous mass extinction.

Members of the subclass Ammonoidea are molluscs with planispirally coiled shells that have radially folded septa. The distinctive folded septa allow for relatively easy identification, and ammonoids are commonly used as index fossils for the Mesozoic.

Raup (1966, 1967) used gastropods and coiled cephalopods to study theoretical shell morphology. His early computer simulations demonstrated that these molluscs used only a fraction of the possible shapes available in nature. His works further showed that two variables, expansion rate and distance of the aperture from the axis, could be used to simulate the variation in planispirally coiled shells (Figure 2). The expansion rate (W) ranges from no expansion (see top row of Figure 3), which would appear as a coiled cylinder, to rapid expansion (see bottom row of Figure 3), which would appear as a coiled, expanding cone. The distance between the aperture and the axis (D) measures how rapidly the coil spirals away from the center of the ammonoid. Raup (1967) used illustrations from the *Treatise on Invertebrate Paleontology* (Arkell et al., 1957) to obtain nonrandom samples for analysis. Further, only the best illustrations were used for calculating ammonoid dimensions (Raup, 1967).

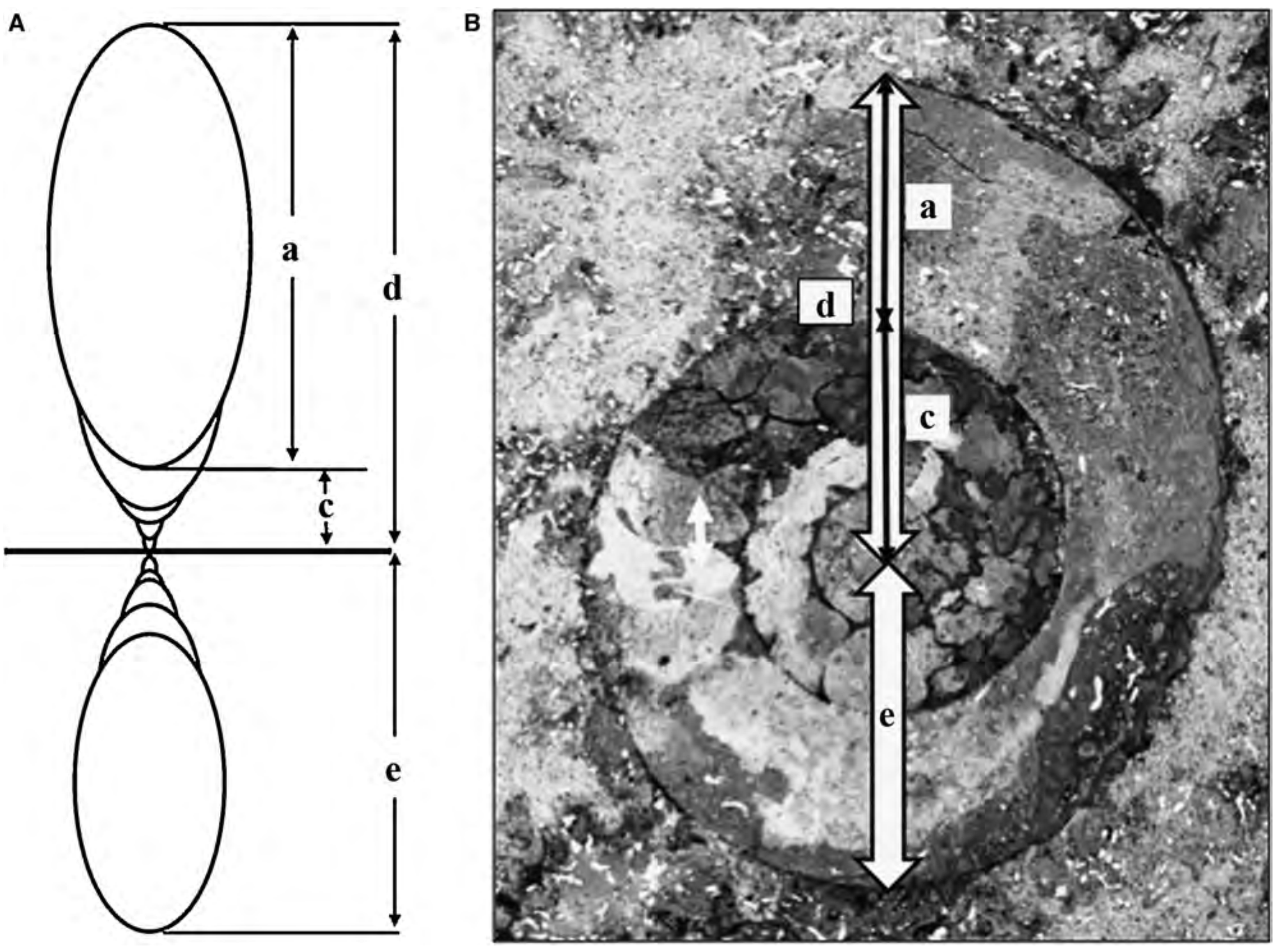

Figure 2. Measurement of ammonoid shell geometry. "A" is from Raup (1967), and "B" is a sample from the beige Jura limestone from Southpark Mall.

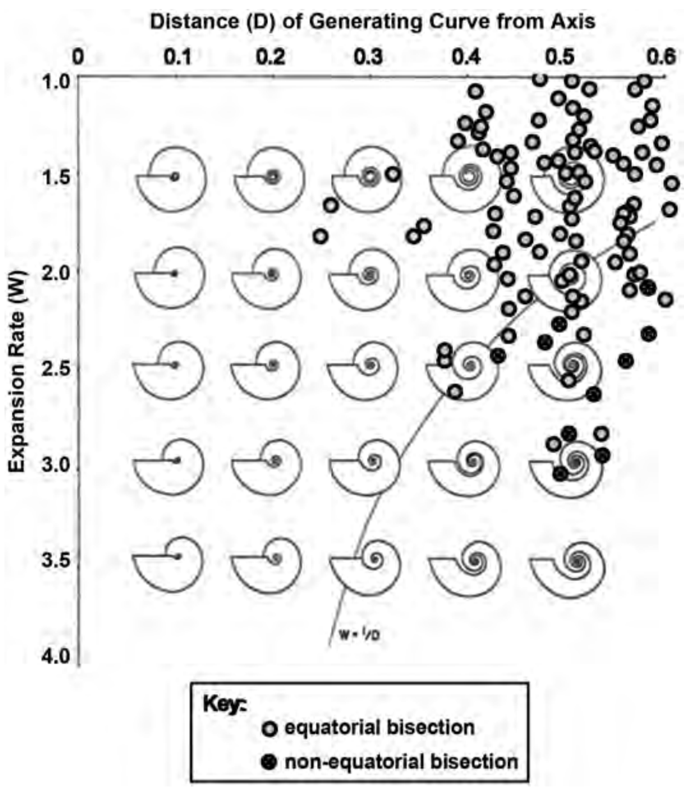

Figure 3. Whorl expansion rate (W) and the distance between the generating curve and the axis of coiling (D) for the ammonoids measured in the light tan limestone flooring tile (data plotted on text figure 3 in Raup 1967).

Raup (1967) determined that the shape of >405 genera of extinct ammonoids clustered around a geometry of W = 2 and D = 0.35. This morphology was largely the result of the need for a shell with whorls that are reinforced by being in contact with each other in a closed spiral and the elimination of hydrodynamic drag from open space between the whorls (Raup, 1967). Measurements of W and D were also important morphological variables for creating models to determine drag coefficients and flow patterns in the research presented by Chamberlain (1976).

For proper analysis of shell geometry, a data set must fulfill several requirements. First, for measurement of the internal shell dimensions, the specimen to be measured must be visible from an angle that is perpendicular to the coiling axis. Second, it is preferable (but not necessary; see Raup, 1967) that the interior of the shell is visible in cross section so that the exact distance between the coiling axis and the point on the generating curve closest to the axis can be determined (an equatorial section). If the interior of the shell is not visible, for example, this location must be inferred, and previous studies have used the distance between the coiling axis and the umbilical seam (Raup, 1967). Raup (1967, p. 45) commented that "it is often impossible to estimate the shape of the non-existent portion of the generating curve" when measuring shell geometry; nevertheless, the use of ammonoids that have been cut lengthwise and cross sectioned as part of the manufacture of the building stones presented in this study minimizes this problem.

○ Activity, Results, & Discussion

The underlying goal of this project was to teach students about ammonoid coiling strategies by having them measure ammonoid cross-sectional geometry and calculate the variety of coiling approaches, W and D. A second goal included having the students compare their results with those presented for samples taken from the *Treatise on Invertebrate Paleontology* (Arkell et al., 1957), presented in the important precedent work by Raup (1967) and discussed in Chamberlain (1976).

To conduct this analysis, the instructor subdivided the floor space at the retail center into corridors so that students would never be sampling (measuring) the same ammonoids. In a class of 20 students, each student was assigned a corridor named after an anchor store.

Students were required to take all the following measurements for each appropriate ammonoid in their assigned floor space (a, c, d, e; Figure 2) and calculate W and D. Students were also required to subdivide their data between dark blue-gray and light beige limestones. The value of W is $(d/e)^2$, and that of D is (c/d). These values of W and D were then compared by the students with those presented in Raup (1967) and plotted on Raup's text figures 3 and 4.

After characterizing the range of variation in spiral form for these ammonoids, the data set was analyzed with respect to four criteria: (1) shell strength, (2) shell streamlining and hydrodynamic performance, (3) carbonate efficiency, and (4) ammonoid stability. The range of variation in form was also evaluated with respect to earlier reported taxa from Raup (1967) to see whether it was possible to determine the ammonoids' ontogeny on the basis of their cross-sectional geometry. Finally, it was hoped that the different groups of ammonoids could be differentiated between the two varieties of limestones used on the property, assuming that they came from different localities or formations.

○ Student Interpretations

Four hundred ammonoid cross sections were measured and plotted in this study. A sample student data chart is presented as Table 1, and a representative fraction (one-third) of the data is presented in Figures 3 and 4. Raup (1967) found that the majority of his 405 genera of ammonoids clustered around a geometry of W = 2 and D = 0.35, whereas those from the Southpark Mall had a similar expansion rate but a greater distance from the generating curve from the axis, and the data tended to cluster around W = 1.9 and D = 0.5. Also, 69.8% of the ammonoids from the Southpark Mall fell within the abundance contours presented by Raup (1967; Figure 5), and 78.8% plotted above the W = 1/D line. Those values that fell below the W = 1/D line (Figures 3, 4, and 5) were primarily the result of poorly selected specimens.

Raup (1967) and Chamberlain (1976) found that the W = 1/D threshold represents the point at which the contact and overlap between successive whorls is eliminated and shell strength and streamlining is diminished. However, the data plotted below the W = 1/D in the present study and artificially high expansion ratio probably represent poor sample selection. Ammonoids that were not bisectioned through the plane of symmetry will have artificially inflated expansion ratios because the full (maximum) dimensions of the chambers are not being measured (Figure 6). This error in

Table 1. Sample student data sheet describing the coiling dimensions of the ammonoids from Southpark Mall.

Store	Limestone	a	c	d	e	W	D
(XXXX)	Light Beige	14	18	33	24	1.89	0.55
(XXXX)	Light Beige	18	22	40	27	2.19	0.55
(XXXX)	Light Beige	14	21	35	27	1.68	0.60
(XXXX)	Light Beige	17	23	40	37	1.17	0.58
(XXXX)	Light Beige	20	24	44	34	1.67	0.55
(XXXX)	Light Beige	15	15	30	22	1.86	0.50
(XXXX)	Light Beige	17	17	34	24	2.01	0.50
(XXXX)	Light Beige	41	19	60	44	1.50	0.32
(XXXX)	Light Beige	21	20	41	39	1.10	0.49
(XXXX)	Light Beige	26	25	51	36	2.01	0.49
(XXXX)	Light Beige	20	22	42	29	2.10	0.52
(XXXX)	Light Beige	25	27	52	40	1.69	0.52
(XXXX)	Light Beige	39	29	68	54	1.59	0.43
(XXXX)	Light Beige	26	25	51	30	2.89	0.49
(XXXX)	Light Beige	24	26	49	34	2.09	0.51
(XXXX)	Light Beige	25	24	49	35	1.96	0.49
(XXXX)	Blue-gray	21	19	40	25	2.56	0.48
(XXXX)	Blue-gray	20	20	40	31	1.66	0.50
(XXXX)	Blue-gray	16	21	37	31	1.42	0.57
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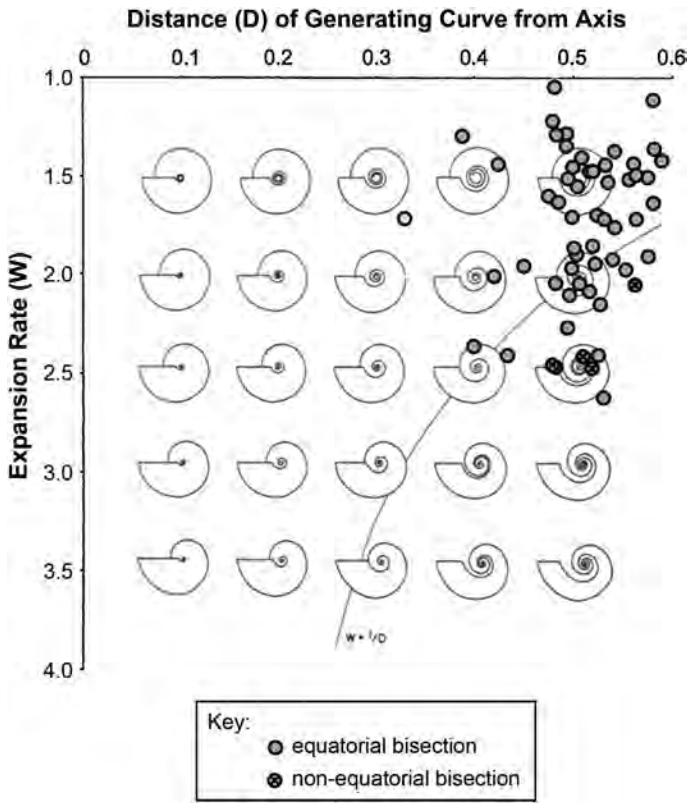

Figure 4. Whorl expansion rate (W) and the distance between the generating curve and the axis of coiling (D) for the ammonoids measured in the blue-gray limestone flooring tile (data plotted on text figure 3 in Raup 1967).

measurement could be predetermined when ribs or ornamentation of the shells were visible in the internal whorls when viewing the cross sections.

As the distribution of ammonoid geometries presented in Figures 3, 4, and 5 suggests, there are environmental restrictions on shell shapes, and the ammonoids used only a fraction of the total geometric continuum available. As shells cross the W = 1/D line, the contact and overlap between successive whorls are eliminated, perhaps leading to a severe decrease in shell strength and the efficiency of the use of shell building materials (Raup, 1967). The limit of W is also related to a combination of stability, attitude, carbonate efficiency, and body-chamber length (Raup, 1967). Chamberlain (1976) further pointed out that as W increased, shell inflation – and, thus, drag coefficient – resulted. Drag is also increased significantly by whorl offlap (Chamberlain, 1976). In summary, Chamberlain (1976, p. 560) stated that "Increase in drag coefficient with W is due to increase in frontal area and relative size of the aperture. Increase in drag coefficient with D is due to increase in the size of the umbilicus."

There was little apparent difference between the geometry of the ammonoids found in the blue-gray and beige limestones (Figures 3 and 4; Tables 2 and 3). The number and distribution of other fossils (primarily belemnoids and bivalves) were also similar between the two varieties of rock.

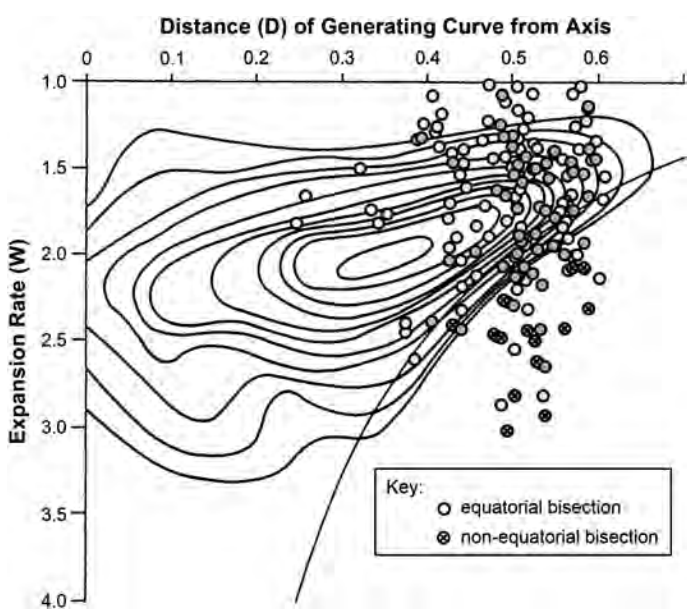

Figure 5. Composite data of ammonoid coiling strategies plotted on the contour intervals (presented as text figure 4 in Raup 1967).

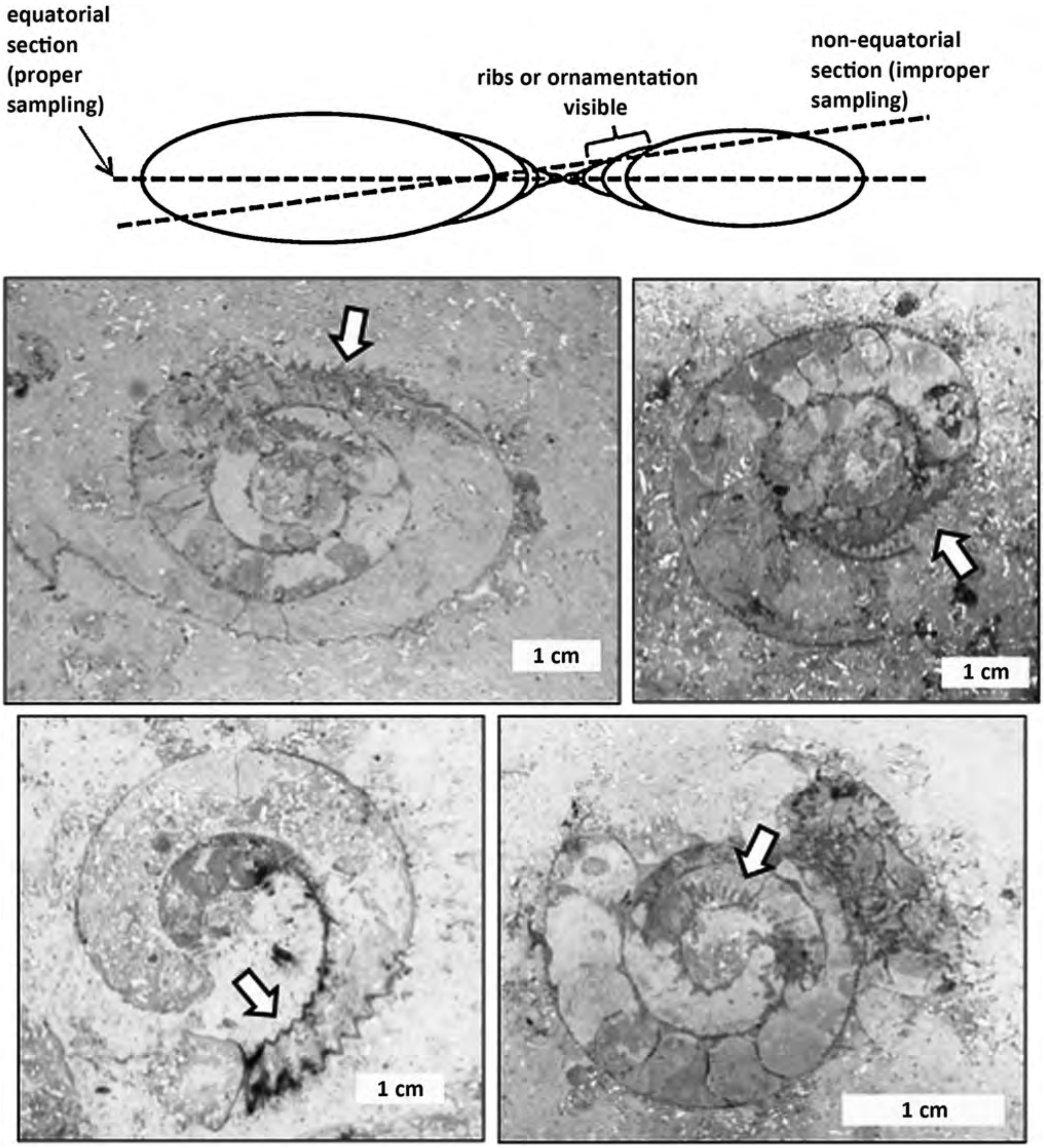

Figure 6. Potential error in sampling occurred when students measured ammonoids that were not cross sectioned through the plane of symmetry. This led to artificially high values of W (whorl expansion rate) and could be detected by the presence of ribs or ornamentation on the exterior of the shell on the inner or outer whorls (indicated by arrows).

A general description of the ammonoid dimensions present in the tile, as well as the internal geometry, is presented in Tables 2 and 3, respectively. The mean ammonoid diameter in the light beige limestone was 77 mm, the maximum diameter recorded was 122 mm, and the smallest diameter was 43 mm. The mean ammonoid diameter in the blue-gray limestone was 79 mm, the maximum diameter recorded was 158 mm, and the smallest diameter was 46 mm. Coiling geometries were also similar, with average W and D values of 1.79 and 0.52 for the light beige limestone and of 1.76 and 0.50 for the blue-gray, respectively.

Table 2. General description of the ammonoid dimensions present in the flooring tile of Southpark Mall.

		Ave.	Min.	Max.	Ave.	Min.	Max.	Ave.	Min.	Max.	Ave.	Min.	Max.
Limestone Variety	**n =**	**a**	**a**	**a**	**c**	**c**	**c**	**d**	**d**	**d**	**e**	**e**	**e**
Light Jura Beige	319	21.8	6	41	22.2	12	35	43.6	23	68	33.2	20	54
Dark Jura Blue-gray	81	21.9	12	46	22.8	3	46	45.4	26	92	34.0	20	66

Table 3. General description of the ammonoid geometry present in the flooring tile of Southpark Mall.

Limestone Variety	Ave. diameter	Min. diameter	Max. diameter	Ave. W	Min. W	Max. W	Ave. D	Min. D	Max. D
Light Jura Beige	76.8	43	122	1.79	0.68	2.89	0.52	0.26	1.00
Dark Jura Blue-gray	79.4	46	158	1.76	1.05	2.56	0.50	0.33	0.57

Of the 400 ammonoids measured by the students, 319 were found in the light beige limestone (79.8%) and 81 were found in the blue-gray limestone (20.2%). This distribution closely mirrors that of the tile surface area and, thus, the sampling region (estimated 80% light beige tile and 20% blue-gray tile), suggesting that relative ammoniod abundance is consistent between the different limestones.

○ Conclusions & Implications for Instruction & Learning

The Southpark Mall, as well as numerous other public localities across the eastern United States, offers a data set of cross-sectioned ammonoids that can be used to measure shell geometry and teach functional morphology to undergraduate and high school students. This valuable, if underappreciated, data set can be compared with earlier important work on cephalopod geometry presented in manuscripts such as those of Raup (1967) and Chamberlain (1976), allowing students to compare their own measured and compiled ammonoid data set with the data in the literature. In addition, the larger data set is readily available to the public and did not require the cutting, cross sectioning, and destruction of fossil specimens.

Such a diverse data set would prove useful for study by secondary school students as well. Research projects might compare the size of the ammonoids between the two types of limestone, for example. Research projects might also focus on fossils other than the ammonoids, including the orientation of the belemnoids (multiple specimens on single tiles appear, upon preliminary analysis, to be oriented in a similar direction and not randomly, suggesting post mortem modification and alignment by water currents) or an analysis of the ratio of the ammonoids to the belemnoids between the limestones. The data set might also prove useful for inclusion in studies that high school students are already familiar with (e.g., species diversity estimates or estimates of biomass/m^3 of past oceans). For younger students, simple identification and counting of the variety of fossils might be instructive, as the fossils are so easy to find and the study area does not have many of the potential hazards found at rock outcrops or quarries. Other pedagogical exercises might involve having students use the ammonoid and belemnoid characteristics to determine the age of the flooring tile.

Students found that the majority of the ammonoids present in the tile of Southpark Mall fell within the abundance contours presented in Raup (1967; Figure 5) and that there was little difference between the ammonoid geometry between the two varieties of tile. Those ammonoids that fell below the W = 1/D threshold probably reflect poorly selected specimens that did not represent an equatorial cross section.

Learning outcomes were threefold for this exercise: (1) students increased their understanding of functional morphology and growth strategy of ammonoids, especially with respect to hydrodynamic streamlining and swimming stability; (2) students compared their findings with earlier reported findings related to ammonoid coiling strategies, allowing students to both critique the earlier work and gain insights into the methods and limits of the scientific method in the historical sciences; and (3) students learned about proper specimen selection to avoid data-set contamination and sampling error. Finally, students gained a sense of ownership and immersion in the scientific process when comparing their own data with those presented in the influential work of David Raup in the *Journal of Paleontology* (1967).

References

Arkell, W.J., Kummel, B. & Wright, C.W. (1957). Cephalopoda, Ammonoidea. In R.C. Moore (Ed.), *Treatise on Invertebrate Paleontology*. Lawrence, KS: Geological Society of America and University of Kansas Press.

Balsam, W.L. & Vogel, S. (1973). Water movement in archaeocyathids: evidence and implications of passive flow in models. *Journal of Paleontology*, *47*, 979–984.

Chamberlain, J.A. (1976). Flow patterns and drag coefficients of cephalopod shells. *Palaeontology*, *19*, 539–563.

Fazio, R.P. (1981). Urban geology. *Science and Children*, *18*(8), 14–15.

Fazio, R.P. & Nye, O. (1980). Making 'rock hounds' of 'city slickers.' *Science Teacher*, *47*(2), 21–23.

Horenstein, S. (2008). Building stone treasure troves. *Evolution: Education and Outreach*, *1*, 520–530.

Kummel, B. & Lloyd, R.M. (1955). Experiments on relative streamlining of coiled cephalopod shells. *Journal of Paleontology*, *29*, 159–170.

Prothero, D.R. (1998). *Bringing Fossils to Life: An Introduction to Paleobiology*. Boston, MA: WCB/McGraw-Hill.

Raup, D.M. (1966). Geometric analysis of shell coiling: general problems. *Journal of Paleontology*, *40*, 1178–1190.

Raup, D.M. (1967). Geometric analysis of shell coiling: coiling of ammonoids. *Journal of Paleontology*, *41*, 43–65.

Savarese, M. (1992). Functional analysis of archaeocyathan skeletal morphology and its paleobiological implications. *Paleobiology*, *18*, 465–480.

Stanley, S.M. (1970). Relation of shell form to life habits in the Bivalvia (Mollusca). *Geological Society of America Memoirs, No. 125*.

Stanely, S.M. (1975). Why clams have the shape they have: an experimental analysis of burrowing. *Paleobiology*, *1*, 48–58.

Stearn, C.W. & Carroll, R.L. (1989). *Paleontology: The Record of Life.* New York, NY: Wiley.

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