MORPHOTYPE MATTERS: AN EXPERIMENTAL ANALYSIS OF THE MORPHOLOGICAL FIDELITY OF GASTROPOD STEINKERNS

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ABSTRACT

Gastropods are commonly preserved as steinkerns (internal casts), a mode of fossilization that leads to loss of external morphological features. This loss of information is problematic for taxonomic identification and ecological inference in evaluating assemblages where original shell material is not preserved. We seek to quantify how closely gastropod steinkerns represent the morphology of their original shells. We investigated this relationship experimentally by fabricating steinkerns in silicone from modern gastropod shells and comparing their geometry to that of the shells we used to create them. In addition to recording traces of ornamentation such as ribs and spines, we used a theoretical morphospace framework to evaluate the fidelity of shell-coiling parameters in steinkerns. Our results show that some morphotypes reflect their taxonomic identification more accurately than others, indicating that steinkern fidelity is highly variable. Experimental steinkerns consistently cluster less reliably by morphotype than their original shell counterparts. Additionally, we find that shell thickness is an important factor in determining steinkern fidelity. The fidelity of the high-spired *Duplicaria duplicata*, for example, is significantly lower than the average value for the morphotypes investigated whereas the fidelity of planispiral *Haplotrema concavum* and open-coiling *Epitonium* is significantly higher, a trend related to shell thickness. Thus, taxonomic identification and subsequent analyses, such as community composition, of steinkern assemblages must recognize this differential fidelity to counter preservational biases.

INTRODUCTION

Morphology is a first-order line of evidence for paleontologists. The shapes of fossils reveal evolutionary histories of ancient organisms and allow investigators to analyze form and function, phylogenetic relationships, and preservational conditions. Yet fossil morphology is subject to taphonomic bias, as clearly evidenced by two types of fossilization for gastropods: preservation of the shell (biomineralized part), and preservation of internal casts called steinkerns, which occurs when sedimentary matrix or precipitated material infiltrates a shell forming a cast that remains when the shell is destroyed. We focus on gastropod steinkerns but other mollusks, including bivalves and cephalopods, are also subject to steinkern-style preservation (Henderson and McNamara 1985). Steinkerns have been used as an alternative to biomineralized gastropod fossils to study a wide range of topics including assemblage composition (Harzhauser and Fehse 2007), evolutionary dynamics (Roy 1994), trace fossils (Vinn et al. 2014), ecology and ontogeny (Nützel 2014), body size (Brayard et al. 2010), and taphonomic biases (Dattilo et al. 2016). A full understanding of the nature of steinkerns is necessary to establish a complete picture of gastropod paleoecology and evolution because the likelihoods of original shell and steinkern preservation vary between depositional environments and are generally inversely correlated. This differential preservation is controlled by a variety of factors including salinity (sulfate content), bioturbation, aragonite saturation, energy, and rate of burial (Wright et al. 2018) and has the potential to substantially impact evidence of diversity. Bush and Bambach's (2004) model of aragonite dissolution bias, for example, showed that in 79 level-bottom Paleozoic assemblages, alpha diversity may be underestimated by up to 29% due to the preferential dissolution of aragonitic gastropods and other fossils composed of the mineral. Thus, steinkerns serve as important evidence for interpreting community composition under conditions where original or mineral-replaced shell material is not preserved, and systematic exclusion or misidentification of steinkerns leads to bias (Cherns and Wright 2009).

Although gastropod steinkerns are common in shallow marine sediments and have been used historically for identification and taxonomy (Knight 1941), they remain under-utilized due to the challenges inherent in the loss of external features typically used for identification. When gastropods are preserved as internal casts, details of their external morphology such as spines and ribs are lost. Without experimental data it is not known to what extent traces of these features are evident on a steinkern. Additionally, taphonomic trends vary by shell morphotype, resulting in bias, but the nature and extent of this bias remains unexplored for most gastropods. Small Cambrian conical shells (not necessarily gastropods), for example, are preferentially preserved as phosphatic steinkerns (Creveling et al. 2014). The influence of morphotype on ease of sediment infill results in distortions of relative abundance among ammonoid and nautiloid steinkerns, a comparable example of the problem investigated here, although those shells contain septa throughout the body chamber that most gastropods lack (Henderson and McNamara 1985; Anderson and Allmon 2018). Thus, even though gastropods are the most diverse group of mollusks with over 60,000 modern species and an extensive fossil record (Bouchet et al. 2017), our understanding of their past diversity is compromised because the fidelity of key morphological characteristics in steinkerns is unknown. Experimental approaches are crucial to quantifying bias in steinkern assemblages.

In addition to biodiversity, gastropod ecology can be inferred from morphology (Pietsch et al. 2021, Vermeij 2022). Experiments have shown that surface varices help *Ceratostoma foliatum* land upright from a fall via hydrodynamic stabilization (Palmer 1977) and observations of extant turritelliforms, i.e., “high-spired, many-whorled shells lacking an aperture elongated by an extended siphonal canal" (Signor 1982), show that surface features and aperture properties differ in burrowing, mobile, and sedentary examples. However, five generalized rules for interpreting gastropod mode of life in relation to the substrate, center of gravity, and respiration based on aperture angle and shape were outlined by Linsley (1977) based on observations of modern marine taxa and these can largely be applied to steinkerns.

Here we investigate the fidelity of preserved morphology evident in steinkerns versus shells. We use modern gastropods to create artificial steinkerns and develop morphometric methods to quantify shell shape using a classic theoretical morphospace model (Raup 1966) in order to compare the coiling geometries of steinkerns to those of shells. This approach has implications for documenting the eco-evolutionary history of gastropods as shell coiling is not only an identifying morphological feature but also provides ecological signals related to form and function (Vermeij 1971; Clements et al. 2008; Johnson 2020).

MATERIALS AND METHODS

Gastropods grow by accretion, depositing material along the mantle edge while coiling around a central axis. A range of isometric theoretical gastropod shell shapes can be described by three parameters: translation rate, distance from the coiling axis, and whorl expansion rate (Raup 1966). We landmarked images of gastropod shells and artificial steinkerns (Fig. 1), used Raup's (1966) original equations to derive these three parameters (see Gerber 2016 for alternative morphospace techniques), and then quantified how much artificial steinkerns deviate from their corresponding shells using the Gower coefficient (Gower 1971) and hierarchical clustering analysis.

We used ten specimens of each of twelve different morphotypes of modern gastropods from the Yale Peabody Museum Invertebrate Zoology (YPM IZ) collections (Table 1). All specimens belonged to old, under-utilized collections with inadequate locality data and all individuals selected are represented by multiples. In contrast to CT scanning, our experimental method has the advantage of producing high-fidelity, physical 3D objects in a way that mechanically emulates natural steinkern preservation (Fig. 2). Further, data collection from 2D photos of 3D objects allows this method to be readily applied to fossil specimens (Figs. S1, S2). To sample specimens with a wide range of morphological properties that might affect preservation potential, we chose a broad but non-exhaustive list of morphotypes—morphologies with stereotyped, generalizable coiling patterns (Table 1). Although there is no consistent set of gastropod morphotypes defined in the literature, the morphotypes included in this study are loosely based on those outlined by Tryon (1882). Shells were imaged with the coiling axis both parallel (apertural view) and perpendicular (umbilical view) to the camera (Fig. 1). To create silicone internal casts, a hole was made in the apex of each shell to allow silicone to fully infiltrate the hollow space. The shells were put in cups filled with Anchor Seal tin-cured GI-1000 silicone molding rubber and placed in a vacuum chamber. After the silicone had set, the shells were cut out of the silicone and the original shell material was dissolved using hydrochloric acid thereby creating artificial steinkerns (here termed “silikerns”). The silikerns were subsequently imaged in the same views as the original shells (Fig. 3).

Morphometric landmarks were placed on images of shells and silikerns at homologous points on each whorl (along sutures for closed coiling geometries) using the ruler tool in Adobe Photoshop (Fig. 1). Raw data were collected in apertural view to calculate translation and whorl expansion rate, and in umbilical view to calculate distance from the coiling axis. Ratios of landmark coordinates were used to calculate translation (T), distance from the coiling axis (D), and whorl expansion rate (W) following Raup (1966):

$$T = (y_{\theta+2\pi} - y_{\theta}/ x_{\theta+2\pi} - x_{\theta}) \tag{1}$$

$$D = a/b \tag{2}$$

$$W = (x_{\theta}/x_{o})^{2\pi/\theta} \tag{3}$$

where *y* is vertical distance between apex and landmark, *x* is horizontal distance between apex and landmark, *a* is distance between coiling axis and inner edge of whorl, and *b* is distance between coiling axis and outer edge of whorl. Differences in measurements within individuals were averaged over successive whorls to produce a single value for T, D, and W for each specimen. This dataset was then plotted in 3D morphospace (sensu Raup 1966) to facilitate analysis (Figs. S3, S4). We were not able to place landmarks on the original shell images of Morphotype 12 (*Monetaria caputserpentis*) because only the final whorl was visible, so this species was excluded from quantitative analysis. However, the artificial steinkern it produced could be measured and its unusual morphology makes it an interesting case to demonstrate the range of information that can be obtained from steinkerns.

The differences in T, D, and W between all shells and silikerns were quantified using the Gower coefficient, which produces a square distance matrix. Two sets of analyses were conducted on this distance matrix. The first tested the null hypothesis (H_0) that there were no significant differences in silikern fidelity between the different morphotypes. To achieve this, the distance separating each silikern from its source shell was isolated and randomly subsampled with replacement 10,000 times, generating 10 silikern-shell distances each time to match the number of silikerns for each morphotype in the dataset. These 10-distance subsamples were then averaged, producing a null distribution of 10,000 silikern-shell distances. This was used to derive the probability of randomly sampling 10 silikerns with equivalent or worse fidelity than the 10-silikern samples of each morphotype (i.e., the p-value), defined as the proportion of random subsamples with equivalent or greater average silikern-shell distances than each morphotype. We then repeated this analysis to test for significant differences in silikern fidelity between genera. However, as most of the genera we sampled belong to a unique morphotype, these results mostly duplicate those of the previous analysis. As such, we do not discuss them (but see Figs. S5, S6).

The second set of analyses sought to quantify the impact of using casts instead of shells in studies of fossil taxonomy, which usually rely on comparative anatomy to group morphologically similar organisms into taxa. Agglomerative hierarchical clustering algorithms apply a similar logic; at each step, they identify the pair of elements, which can be individual points or clusters, separated by the shortest distance and group them together in a new cluster. This process is repeated in a stepwise fashion until the entire dataset has been classified. When applied to morphological distance matrices, these algorithms group taxa together based upon their anatomical similarity, just as taxonomists do when classifying fossil taxa. As such, we consider it reasonable to assume that anything that compromises the performance of hierarchical clustering algorithms will also increase the likelihood of misclassification in taxonomic studies restricted to morphological data.

To test the impact of this effect on casts versus shells, we separated the distance matrix into two submatrices: one containing all silikern-silikern distances, the other containing all shell-shell distances. 10,000 subsamples of the shell-shell submatrix, each of which contained 55 shells (i.e., 50% of the total number), were randomly drawn without replacement to ensure the dendrograms produced by the hierarchical clustering analysis contained equal numbers of tips. Subsamples of the silikern-silikern submatrix were then drawn to match. Complete linkage hierarchical clustering (also known as farthest neighbor clustering) was then used to analyze these subsamples and the complete shell-shell submatrix. The result was 10,000 dendrograms representing the silikern subsamples, 10,000 representing the shell subsamples, and a final dendrogram representing all shells in the dataset that we used as our reference point for evaluating how well subsamples of casts and shells preserve a clustering pattern. The difference between the reference dendrogram and that of each subsample was then quantified using the clustering information distance (CID), a reliable, efficient, and unbounded metric that quantifies differences in branching order (Smith 2020a). The greater the CID, the greater the number of topological discrepancies between the dendrograms, and so the greater the likelihood of erroneous classification. The CID distributions of the two sets of subsamples were then compared. These analyses were then repeated to test whether using casts differentially compromised the ability of hierarchical clustering analyses to correctly group genera and morphotypes. However, these results (Figs. S7, S8, S9) were not informative due to the representation of most morphotypes by a single genus, and we do not discuss them. All analyses were conducted in R (R Development Core Team 2022) using base R, Plotly (Plotly Technologies, Inc.), vegan (Oksanen et al. 2022), ape (Paradis and Schliep 2019), and TreeDist packages (Smith 2020b) functions (see Supplementary Information for further details).

Repositories and institutional abbreviations— Yale Peabody Museum Invertebrate Paleontology (YPM IP), Yale Peabody Museum Invertebrate Zoology (YPM IZ).

RESULTS

Surface Features

Our experiments provide evidence that surface traces on steinkerns can reflect external shell morphology. Two main types of ornamental features, spines and ridges, appear on silikerns as three-dimensional structures (Fig. 2). Where a vertical row of three prominent spines is present on one whorl of a *Siratus articulatus* specimen, the corresponding silikern shows only a small, vertically oriented raised feature. Inflection points of the curvature of this feature represent horizontal ridges on the original shell where each spine meets the body of the shell, so the precise location of spines can be determined from the silikern (Fig. 2A). There is no evidence of spines on whorls closer to the apex of the silikern, where spines are smaller on the original shell. Observations of fossil steinkerns reveal analogous surface features, which indicate the presence, general nature, and location of external ornamentation on the original shell, though, as in our experimental silikern, this information is limited. The outermost whorls of *Sinistrofulgur perversum* retain parallel grooves running perpendicular to the aperture (Fig. 2B). Although we have not observed evidence of this feature on a fossil steinkern, it likely could be fossilized in a similar manner to the spine rows. Previous observations of surface features on gastropod steinkerns have yielded information on the morphology of the shell (Mackinnon 1985), but this is the first experimental evidence linking steinkern features to external shell features.

Silikerns also reveal details beyond those of the original shell. Although Raup parameters could not be determined from the original shell of *Monetaria caputserpentis*, silikerns reveal the coiling pattern of this species (Fig. 3L). The columellar and labral teeth of the original shell are reflected in grooves near the aperture of the silikern, and similar structures are evident on the surface of some steinkerns (Fig. 2D).

Steinkern Fidelity

All three coiling parameters show differences in fidelity as revealed in the silikerns of different morphotypes (Figs. 3, 4, S3, S4, S10). Of the 11 morphotypes tested, only Morphotype 2, the high-spired *Duplicaria duplicata* (Fig. 3B), presents significantly greater silikern-shell distances relative to the null distribution ($p < 0.0001$), indicating that silikerns of this morphotype have particularly low coiling parameter fidelity (Fig. 5A). In contrast two morphotypes, numbers 6 (*Haplotrema concavum*, a nearly planispiral taxon, Fig. 3F) and 11 (*Epitonium*, an open-coiling taxon, Fig. 3K), present significantly smaller silikern-shell distances ($p = 0.0110$ and 0.0077 respectively), demonstrating relatively high coiling parameter fidelity (Fig. 5A) (applying a threshold of $p < 0.05$ to the number of random subsamples with equivalent or smaller silikern-shell distances instead of greater). Although it does not breach the $p < 0.05$ threshold, Morphotype 8 (*Siratus articulatus,* Fig. 3H) also demonstrates good fidelity, as only 529 of the 10,000 random subsamples present smaller average silikern-shell distances ($p = 0.0529$).

Impact on Hierarchical Clustering

The clustering information distance (CID) separating the silikern clustering from the reference pattern is greater than that separating the shell clustering across all subsamples, indicating that silikerns consistently introduce more error into hierarchical clustering analyses than shells (Fig. 5B). On average, the silikern CIDs are about three times greater than the shell CIDs, with means of 32.7 and 10.3 and medians of 32.7 and 10.4 respectively.

DISCUSSION

The power of steinkerns to record evidence of external ornamentation and reveal ecological and evolutionary information has been historically underestimated. Our experiments demonstrate that surface marks on steinkerns can be used to infer the presence and nature of external features, which are often used in taxonomic identification. Additionally, our experiments revealed the coiling pattern of *Monetaria caputserpentis,* which is obscured by the external shell morphology (Fig. 2D). Fossil gastropod phylogenetics are heavily based on morphology (Wagner 2001), so knowledge of the internal structures of taxa with similarly obscured features would add characters of phylogenetic significance. For example, a surface marking similar to that left by the aperture of *Monetaria caputserpentis* on many specimens of *Cassidaria cheops* fossil steinkerns may indicate that this species had an outer whorl similar to that of the cowrie (Fig. 2D). Also, marks that we identify as traces from encrusters that colonized a shell after death were observed on both silikerns and steinkerns (Fig. 2C). If they were indeed created through similar processes, these marks on steinkerns may reveal the biostratinomic history of the specimen. This kind of internal information preserved on steinkerns may provide additional data in some cases.

Calculations of assemblage diversity derived from steinkerns almost certainly underestimate true diversity. Silikerns performed worse than original shells for morphotype clustering using coiling parameters (Fig. 5B). These results likely underestimate the error in using real steinkerns as silikerns are very high-resolution casts, maximizing the detail preserved. This discrepancy illustrates the need for a full understanding of the different fidelity of shells versus steinkerns of different morphotypes. Morphotype 2 (represented by *Duplicaria duplicata*) displayed the lowest fidelity of the morphotypes we investigated. Due to its thick shell, the whorls of this high-spired shell morphotype are in contact in the original shell but not in our silikerns. Open-coiling patterns also occur in high-spired fossil steinkerns (Fig. S11). This major morphological difference between original shell and steinkern is reflected in their measured parameters, causing the discrepancy. This experiment shows that an open-coiled steinkern does not necessarily reflect an open-coiled shell (although some gastropods are open-coiled in life), and open-coiling in the steinkern may represent a significant transition away from the morphology of the original shell and therefore low fidelity.

Both morphotypes with the highest fidelity are thin-shelled: Morphotype 6 (*Haplotrema concavum*) is close-coiled whereas Morphotype 11 (*Epitonium*) is open-coiled but in both cases this morphology is revealed by the silikern. This pattern suggests that thicker shells relative to whorl size (e.g., Morphotype 2) likely lead to less representative steinkerns as opposed to thinner shells (e.g., Morphotypes 6 and 11). Shell morphology in coiling-axis view, used to calculate distance from the coiling axis, is consistently well preserved in Morphotypes 6 and 11, which may also contribute to their high fidelity. In summary, steinkern identification at the assemblage level has great potential but must be conducted in the context of morphological fidelity to avoid the bias inherent in steinkern-style preservation. Identification and morphological reconstruction could also be enhanced by surface features on steinkerns, such as those on our silikerns, that represent external features on the original shell. However, not all types of sculpture are likely to be replicated on steinkerns, as this is influenced by how sculpture develops in different gastropods and whether internal or external remodeling are involved (Anderson and Allmon 2018).

Modern gastropod shells are composed of aragonite or aragonite and calcite (Hall and Kennedy 1967). Aragonite is preferentially and frequently lost due to dissolution, especially in high-salinity environments, so much of the gastropod fossil record relies on steinkern-style preservation (Cherns and Wright 2009). A relationship between morphotype and shell composition has previously been reported in the Pennsylvanian of north-central Texas, where calcified, low-spired euomphalids preserved as shells while aragonitic, medium-spired pleurotomarian gastropods are preserved as steinkerns (Yochelson et al. 1967; Batten 1984; Wagner and Erwin 2006). Furthermore, shifts in dominant aragonite microstructures (from primarily nacreous to crossed-lamellar) that evolved during the Mesozoic Marine Revolution may have contributed to the dominance of high-spired shells (Salinas and Kisailus 2013), but the susceptibility of different aragonite microstructures to dissolution is unknown. Biases in steinkern preservation owing to mineral composition and morphology create additional challenges for investigators who seek to understand assemblage composition and test macroevolutionary hypotheses. However, experiments can be used to understand bias and identify potential identification errors resulting from a lack of external features, thereby increasing the rigor of such interpretations.

Our results identify several areas for further exploration in the use of gastropod steinkerns for ecological and evolutionary studies. We tested Raup's (1966) classic morphometric model which provides a first-order description of shell shape but is not all-encompassing. It is likely that some parameters are more useful for steinkern identification than others. Different approaches that have since been used to quantify shell shape could also be applied to steinkern identification (Urdy et al. 2010; Noshita 2014; Collins et al. 2021). Future work could incorporate additional parameters such as aperture shape and ontogenetic change in non-isometric taxa. Applying similar methods to diverse and disparate modern taxa would allow the impact of shell thickness on the fidelity of coiling parameters to be better quantified, as experiments would reveal which taxa are most likely to leave evidence of shell sculpture on their steinkerns. We investigated patterns of fidelity at the level of shell morphotype, but future studies at the genus or species level might help produce a framework for calculating bias at different taxonomic levels, since closer relatives may be more similar in morphology and thus analyses at lower taxonomic levels may be more susceptible to bias. This is likely a complex trend, as our preliminary analysis shows that the nature of generic differences varies depending on morphotype (Fig. S12). Additional experimentally determined constraints on steinkern fidelity would allow investigators to quantify bias in calculations of community composition across different taxa and morphologies in steinkern assemblages more accurately. Steinkerns represent a valuable and relatively untapped resource for researching the geological history and evolution of gastropods.

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DECLARATION OF COMPETING INTERESTS

The authors declare no competing interests.

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FIGURE CAPTIONS

FIG. 1.—Measurement scheme. A) Aperture view used to calculate translation (T) and whorl expansion rate (W). B) Coiling axis view used to calculate distance from the coiling axis (D). Red dots represent the coiling axis, blue dots represent landmarks.

FIG. 2.—Original shells (left), corresponding silikerns (middle), and steinkerns showing similar characteristics (right). A) Morphotype 8 *Siratus articulatus* (YPM IZ 110139) showing evidence of shell spines on the silikern compared to *Cassidaria cheops* (YPM IP 255138) which preserves similar surface features. B) Morphotype 7 *Sinistrofulgur perversum* (YPM IZ 110127) showing evidence of shell ridges on the silikern. C) Morphotype 4 *Naticarius canrena* (YPM IZ 110149) and *Lanistes sodaensis* (YPM IP 255119) showing traces of encrustation. D) Morphotype 12 *Monetaria caputserpentis* (YPM IZ 110163) showing columellar and labral teeth corresponding to grooves on the silikern compared to *Cassidaria cheops* (YPM IP 255138), which preserves similar grooves. Both fossils are from the Eocene of the Fayum Depression, Egypt.

FIG. 3.—Side-by-side comparisons of the shell and silikern of each morphotype. A) Morphotype 1, *Conus brunneus*, YPM IZ 110115. B) Morphotype 2, *Duplicaria duplicata*, YPM IZ 110121. C) Morphotype 3, *Oliva* sp., YPM IZ 1110133. D) Morphotype 4, *Naticarius canrena*, YPM IZ

110147. E) Morphotype 5, *Rumina decollata*, YPM IZ 110152. F) Morphotype 6, *Haplotrema concavum*, YPM IZ 110157. G) Morphotype 7, *Sinistrofulgur perversum*, YPM IZ 110127. H) Morphotype 8, *Siratus articulatus*, YPM IZ 110139. I) Morphotype 9, *Astraea americana*, YPM IZ 110356. J) Morphotype 10, *Fasciolaria tulipa*, YPM IZ 110348. K) Morphotype 11, *Epitonium* sp., YPM IZ 110192. L) Morphotype 12, *Monetaria caputserpentis*, YPM IZ 110163.

FIG. 4.—Raup parameters for all shells and silikerns of each morphotype. A) Translation. B) Distance from the coiling axis. C) Whorl expansion rate. Differences between the values of shells (blue circles) and silikerns (orange squares) represent differential fidelity by morphotype.

FIG. 5.—Quantitative results. A) Distribution of average silikern-shell distances of 10,000 random samples each consisting of 10 silikerns. Average silikern-shell distances are bounded between 0 and 1. Dashed lines indicate average distances for each morphotype (each represented by 10 specimens). P = p-values. M = morphotype. P-values defined as number of random samples with average distances equal to or greater than that of the morphotype. B) Clustering information distances (CIDs) separating the clustering of subsamples of shells and silikerns from the reference clustering pattern derived using all shells. Each boxplot summarizes l0,000 CIDs: the box delimits the interquartile range, the central line denotes the median, and the whiskers encompass the CIDs that are no more than 1.5 times the interquartile range beyond the upper and lower quartiles.

TABLE. 1.—Taxa used in this study. Twelve morphotypes are represented either by ten specimens each of one genus or five specimens each of two genera, based on specimen availability, with the exception of *Monetaria caputserpentis*, which posed unique difficulties and was excluded from quantitative analysis (see text).