Coiling in gastropods: a lead to synthesis

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Biological structures lie at intersections of function, construction and history. Conversely, the geometry of structures modulates how these three aspects of organic form manifest in different taxonomic groups and ecological circumstances, raising challenges to causal inferences. Here, I apply the familiar logarithmic helicospiral (logspiral) model for coiled shells, to assess its fit to data on gastropod shells and to study allometry, covariation and constraint in coiling behavior, in light of adaptationist and proximate mechanistic explanations. I derive convenient expressions for the three-way relation between expansion rate, apical angle and downward lead angle of spiral paths on shells. Combining several published datasets, I demonstrate that centerline spirals of gastropod shells are well-approximated by isometrically growing conical logspirals. Allometry manifests in the relative growth of apertures. Derived expressions also impose underappreciated covariation in coiling parameters. Specifically, I show that the inverse relation between spire-height and expansion rate, usually attributed to economical and mechanical demands, can equally be explained by taxon-specific lead angles and variation in growth (shell expansion). I further discuss my results in the context of two recently suggested mechanistic drivers of coiling — mismatch of shell and soft-body growth, or differential rates and directions of cellular processes at the mantle edge. More generally, geometry dictates particular "laws of form" for biological structures that have practical use in data analyses and integration and that need to be fully acknowledged when seeking causal adaptationist or mechanistic explanations.

allometry, logarithmic spiral, theoretical morphology, morphometrics, mollusc

Since antiquity, molluscan shells have served as exemplars for the immense variety of nature and, in the past two centuries, to how such diversity can be understood and unified by mathematical modeling (1–4). Conchiferans also feature prominently in discussions of adaptation and constraint, the exchange among functional, constructional and historical aspects of form that is at the core of biology (5). The standard point of departure for modeling coiled shelly forms, both extant and fossil, is the logarithmic helicospiral (hereafter, *logspiral*) (1–4). Logspirals are famously self-similar, maintaining fixed proportions while expanding in size (i.e., isometric growth). Much literature discusses its inadequacy, due to commonly observed ontogenetic allometry (variation in coiling parameters with age or size) and irregular coiling, where even the coiling axis is not fixed (4–7).

A first goal of this work is to assess the nature and magnitude of deviations from isometric growth in gastropod shells, by fitting conical logspirals (Fig. 1*A*,*B*) to available data. One convenient formulation that explicitly accounts for allometry is

$$r = r(\theta) = r_0 e^{\alpha\theta}, \quad z(r) = T r^k, \qquad [1]$$

where r, θ and z define a cylindrical coordinate system, z being the coiling axis of the helicospiral shell (Fig. 1*A*,*B*). The isometrically growing conical shell (1, 3) is a special case, where the allometric relation $z(r)$ degenerates to simple proportionality. The constant T, then, becomes Raup's dimensionless *translation* parameter (3), related to β, the half-apical angle (hereafter, *apical angle*; $T = \cot\beta$; Fig. 1*B*).

A shell, however, is not a single helicospiral, but a three-dimensional structure made of "a bunch" of such spirals — hereafter, *multispiral* approach (Fig. 1*D*; also called multivector; 1, 4, 8). Alternatively, a shell can be described by a *generating curve*, a closed figure that sweeps through space along a logspiral *centerline* (Fig. 1*C*) (1–3). These logspirals share a single common value of expansion rate — α in Eq.[1], or Raup's *whorl expansion rate*, $W = e^{2\pi\alpha}$ (2, 3). By geometric necessity, however, they differ in other parameters (8). Particularly, in apical angle, β, and in the downward *lead angle*, γ (Fig. 1*B*,*D*,*F*,*G*). Expansion rate, α, is typically small (< 0.2) in gastropods (1), resulting in the following expression for the three-way covariation of expansion rate, apical angle and lead angle,

$$\tan\gamma \approx \alpha \cot\beta \qquad [2]$$

(SI). In the words of D'Arcy Thompson, "It seems a complicated affair; but it is only a pathway winding at a steady slope up a conical hill ... a certain ensemble, or bunch, of these spiral curves in space constitutes the self-similar surface of the shell" (1). A second goal is to demonstrate how the above expression for this "steady slope" (lead angle, γ) has underappreciated implications to adaptationist and mechanistic interpretation of covariation in coiling parameters in gastropods.

Results and Discussion

Schindel (10) previously suggested to replace Raup's coiling parameters with other, derived from loglinear regressions of shell width and spire height on revolution angle, θ. In terms of Eq.[1], these regression slopes are given by α and $k\alpha$, respectively. His parameters, therefore, are akin to coefficients of multivariate allometry, though he has not made that link. Schindel noticed that, unlike in Raup's morphospace, in the new parameter space the shells of sixty taxa show strong positive covariation. That is expected according to multivariate allometry, $k\alpha = \alpha$ means isometric growth. Fig. 2*A* presents Schindel's data, in terms of parameters α and k of Eq.[1]. Scatter does not deviate much from isometry ($k = 1$), demonstrating that conical logspirals are reasonable first approximations for gastropod shells. Second, deviations from isometry are almost exclusively biased upwards, towards *doming* ($k > 1$).

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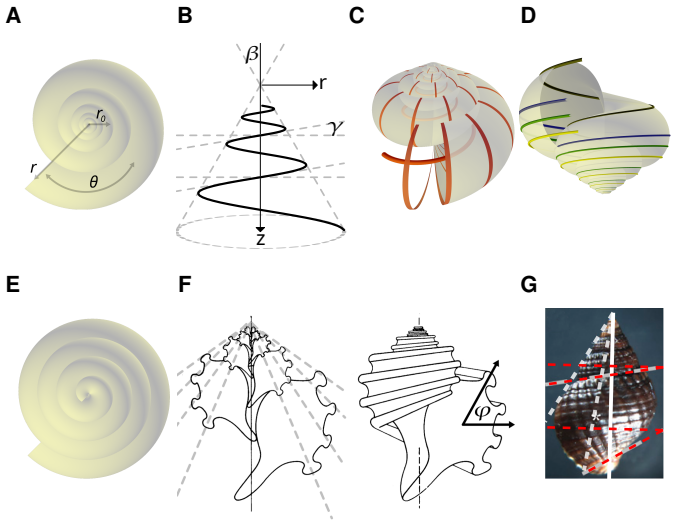

Fig. 1. Theoretical morphology in a snailshell. (*A*) Logspiral shell in apical view. Radius, r, revolution angle, θ, and initial size, $r_0 = r(\theta = 0)$, are illustrated. (*B*) Conical logspiral in lateral view. (Half-)Apical angle, β, and lead angle, γ, are defined. (*C*) Generating curve approach to shell modeling. Shell surface defined by a closed figure (here a circle) that sweeps along a centerline logspiral. (*D*) Multispiral approach to shell modeling, where shell surface is defined by many spiral paths, differing in lead angle. Uppermost (black) spiral most inclined, as it lies closest to the coiling axis. (*E*) Growth map models show that a combination of linear growth (constant growth rate) and a fixed centerline lead angle produces domed shells ($k \approx 2$). But such shells are unnaturally characterized by Archimedean, rather than logarithmic, spirals (SI). (*F*) Helicospirals around a shell can be parametrized by position on the aperture, e.g., azimuth angle φ, demonstrated by adopting the pretty illustrations of *Ecphora* by John S. Spurbeck (2). Apical angle (left) and lead (right) vary among spiral paths. α estimated at 0.152 (slightly higher than Raup's reported value). Measured angles are β = 54.45°, 44.75°, 34.71°, 23.02° and γ = 6.65°, 9.17°, 15.16°, 21.64°. Close to theoretical γ-values (Eq.[2]) of 6.22°, 8.77°, 12.56°, 20.47°, respectively. (*G*) A similar demonstration using the *Tritia* shell from Johnson et al. (9). α = 0.0825°. Upper (suture) spiral: β = 30.61°, γ = 9.7°. Lower (abapical) spiral: β = 9.1°, γ = 30.14°. Again, γ-values close to theoretical values of 8° and 29.51°, respectively, as the conical logspiral model predicts.

More recently, Collins et al. (11) provided a larger dataset containing ontogentic sequences of apertures, obtained from sectioned specimens or microtomography. Fig. 2 presents a reanalysis of their data by first fitting the conical logspiral model to aperture centroids (Fig. 2*C*; SI). Centerline spirals follow the isometric conical logspiral model more tightly than in Schindel's data (Fig. 2*B*; a mixed-effect linear growth model estimated k at 0.94, 95%CI [0.92, 0.96], for *Maoricolpus*, 1 [0.98, 1.02] for the *Tylospira* clade and 0.96 [0.95, 0.97] for the rest of the Struthiolariidae). Comparing expansion rate of aperture sizes to that of centerline radii, α, I find that aperture size grows with positive allometry for *Maoricolpus* (high-spired Turritellidae), but with negative allometry for Sturthiolariidae (allometric exponent of aperture area is 2.1 [2.07, 2.14], for *Maoricolpus*, 1.66 [1.59, 1.73] for *Tylospira* clade and 1.88 [1.85, 1.91] for rest of Struthiolariidae). The effect, in either direction, is weak , but may still correspond to undersecretion and oversecretion of shell material, respectively, relative to soft-body growth, as suggested recently by Chirat et al. (6). Accordingly, *Maoricolpus* are high-spired, and within Struthiolariidae the *Tylospira* clade is relatively low-spired (Fig. 2*D*).

Observed covariation in coiling parameters and uneven distribution in morphospace often receive adaptationist interpretations, such as mechanical strength, postural stability or economical shell construction (3, 12, 13). However, for small α, typical of most gastropods, this covariation may also be explained by seemingly arbitrary conditions on lead angle. For example, Raup's (3) condition for tight coiling, or whorl overlap, given circular apertures, $\sinh(\pi\alpha)\cot\beta < 1$, is practically indistinguishable from the condition $\gamma < \mathrm{atan}(1/\pi)$ (0.318 or 17.66°; Fig. 2*D*; SI). Similar conditions can be formulated for non-circular apertures (Fig. 2*D*; SI). A geometric constraint on lead angle, combined with variation in growth rate (shell expansion), can produce (given Eq.[2]) the empirically observed inverse relation between $\cot\beta$ and α (or Raup's T and W). Fig. 2*E* shows estimates of lead angle for the dataset of Collins et al. (11, SI). Different clades cluster around typical values of γ that seem independent of variation in α. Variation in apical angle ($\cot\beta$) follows as a passive consequence (Eq.[2]) of growth (variation in α) and geometry (lead angle, γ) at the mantle edge.

Growth map models (Fig. 1*E*; SI) and the differential geometry tradition in theoretical morphology (6, 7; Fig. 1*E*; SI) similarly attempt to explain global shell shape by explicitly modeling differential growth rates and directions around a shell's aperture. The latter approach describes shell coiling in terms of *curvature* and *torsion* (in the differential geometry sense) of centerline curves (6, 7). Taking the multispiral standpoint, helicospirals on the shell (Fig. 1*D*), designated by position on the aperture, φ (Fig. 1*F*), differ in torsion-curvature ratios, which are another way to define $\tan\gamma$. A shell's aperture, therefore, dictates a gradient in lead angle (Fig. 1*D,F,G*),

$$\frac{\mathrm{d}\gamma}{\mathrm{d}\varphi} \approx -\frac{\alpha}{\sin^2\beta}\left(\frac{\mathrm{d}\beta}{\mathrm{d}\varphi}\right) \qquad [3]$$

(Eq.[2], SI). This gradient determines how much neighboring helicospirals diverge in lead. Typically, as one moves abapically along the perimeter of the aperture, spirals are initially roughly parallel ($\frac{\mathrm{d}\beta}{\mathrm{d}\varphi}$ vanishes in Eq.[3]; Fig. 1*D*). But as the aperture begins to close, both terms of Eq.[3] become larger, resulting in increasing divergence of spiral paths in both abapical and adaxial direction (Fig. 1*D,F*). That is a direct geometric consequence of logspiral coiling. Rates and directions of cellular growth and division that are correlated with this gradient (7, 9) are, therefore, a null expectation, for both isometric and allometric shell growth. In developmental plasticity parlance, whether the cellular processes are "leaders" or "followers" remains, however, to be determined. Moreover, previously formulated challenges to fine control of global shell form in gastropods by apertural growth rates still remain (14).

Overall, and in the manner of D'Arcy Thompson (1), logspiral geometry dictates particular "laws" for coiled shells. Conical logspirals seem to fit shells of gastropods quite well, particularly, their centerline spirals. Allometry, while common, remains relatively weak. As others before (15), I argue that significant allometry is confined to the protoconch-teleconch transition and, therefore, the geometric apex of conical logspirals of later whorls may not coincide with the actual apex of the shell. If not corrected, that effect may produce overestimates of allometry (e.g., possibly in Schindel's data; Fig. 2*A,B*; SI). This claim should be further

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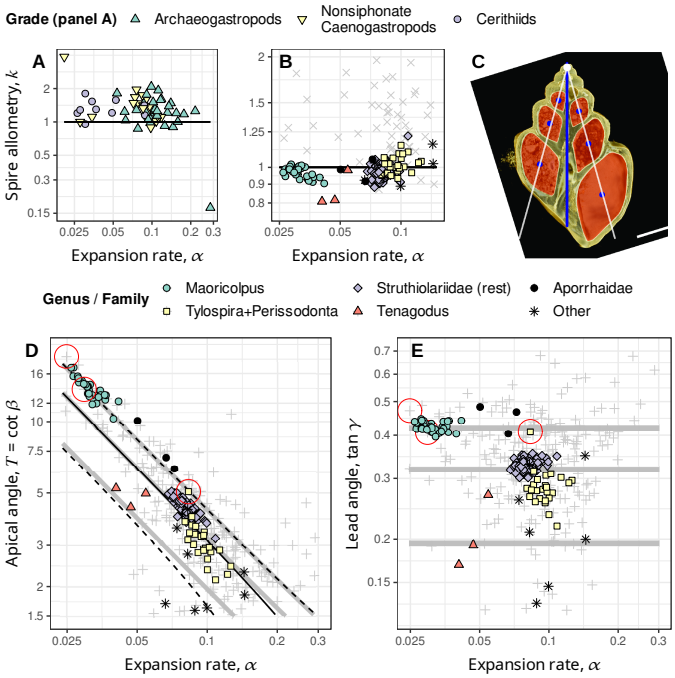

Fig. 2. Empirical covariation of coiling parameters. (*A*) Spire allometry, k, for Schindel's (10) gastropod taxa, divided among his three "grades". With the notable, but unsurprising, exceptions of *Haliotis* and *Truncatella*, scatter does not deviate much from isometry ($k = 1$; solid black). Deviations are biased upwards, towards doming. (*B*) Same for the reanalyzed data of Collins et al. (11). Shells follow the conical logspiral model more tightly than in Schindel's data (in gray). Most notable outliers are shells of the open-coiled *Tenagodus*. (*C*) A sectioned shell of *Tylospira coronata* from the dataset of Collins et al. (specimen P135697h). Illustrated are apertures (red), aperture centroids (blue dots), coiling axis (blue line), estimated apex (white dot) and estimated apical angle (white lines). (*D*) Inverse relationship between spire height, $\cot\beta$ or Raup's T, and expansion rate, α, for the dataset of Collins et al. For reference, data of marine species from Noshita et al.'s (13) survey of coiling parameters is also presented (gray), where values of $\cot\beta$ were converted to represent centerlines (SI). Values for *Turritella rubescens* and *T. fortilirata* (circled red on left) coincide well with the scatter for *Maoricolpus* from Collins et al. Solid black line indicates Raup's (3) whorl-overlap boundary that separates tightly-coiled and open-coiled shells of circular aperture. The fit is not bad, given that actual apertures are not circular. The boundary can be modified (SI) for other aperture shapes (upper dashed line for high-spired *Maoricolpus*) and for open umbilici (Raup's D nonzero; lower dashed line for *Tenagodus*). The single specimen of the recent species *Tylospira scutulata* is highlighted (circled red in center), showing its more fusiform shape, compared to fossil *Tylospira*. Accordingly, it lies on the boundary curve for high-spired Turritellidae. Such boundary curves for tight-coiling, however, are practically indistinguishable from inverse relationships that fixed lead angles in Eq.[2] dictate (gray lines). (*E*) Estimates of lead angle, γ, from aperture centroids. Gray lines represent median values of $\tan\gamma$ for *Maoricolpus* (upper) and *Tenagodus* (lower) and $\tan\gamma = 1/\pi$, for Raup's whorl-overlap condition. Estimates for Noshita et al.'s data were calculated from Eq.[2]. Circled specimens as above. A mixed-effect linear growth model (SI) estimated $\tan\gamma$ at 0.421, 95%CI [0.417, 0.429], for *Maoricolpus*, 0.281 [0.267, 0.294] for *Tylospira* clade and 0.325 [0.322, 0.327] for rest of Struthiolariidae.

scrutinized for terrestrial gastropods, as this study was confined to marine species. More broadly, such geometric relations are useful in data analyses and in combining data from several sources, obtained by different methodologies, as I have shown here (Fig. 2; SI). Adaptationist approaches should similarly acknowledge alternative, often indistinguishable, explanations that emerge from such "laws of form" (Fig. 2*D*,*E*).

Materials and Methods. Images in Fig. 1*F*,*G* from Raup (2) and Johnson et al. (9), reproduced here under fair use and conditions of the PNAS license. Data on coiling parameters was obtained from tables in Schindel (10) and Dryad repositories of Collins et al. (11) and Noshita et al. (13). The latter dataset is augmented with data from a later study, and values of $\cot\beta$ (or T) were converted to represent centerline spirals (see SI). Reanalysis of the Collins et al. dataset included fitting conical logspirals ($k = 1$, Eq.[1]) for each specimen, locating the apex and estimating the apical angle, correcting measured z-values accordingly, estimating coiling and allometry parameters (Fig. 2*B*,*D*,*E*), applying mixed-effect growth models to estimate inter-clade differences in coiling and allometry and generating `svg` images (e.g., Fig. 2*C*) from the original data and `jpg` files, for convenient visual inspection of fitted conical models. More detail in SI.

Data and software availability. All data, code and images (except original images for Fig. 1*F*,*G*) are available at https://doi.org/10.5281/zenodo.15723487. Web app for theoretical morphology of coiled shells (Fig. 1*A*,*C*-*E*) is available at https://doi.org/10.5281/zenodo.15514394

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