Coiling in gastropods: a lead to synthesis

Ido Filin [1] *

[1] Kangasala, Finland

* Corresponding author. E-mail: ido@filin.fi

Running headline: Coiling in gastropods.

Supplementary material: SI appendix.

The author(s) declare(s) no conflict of interest.

This manuscript was compiled on 9 November 2025.

DRAFT

Abstract

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 gastropods, 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 relationship 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 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.

Keywords: allometry, developmental plasticity, theoretical morphology, morphometrics, ontogeny, mollusc, molluscan shell

DRAFT

Introduction

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 (Moseley 1838, 1842, Thompson [1942] 1992, Raup 1961, 1966, Vermeij 1993, Stone 1996, McGhee 1999, Urdy 2015, Hammer 2016). 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 (Seilacher 1973, Savazzi 1990, Vermeij 1993, Edie et al. 2024). The standard point of departure for modeling coiled shelly forms, both extant and fossil, is the logarithmic helicospiral (hereafter, *logspiral*) (Thompson [1942] 1992, Raup 1961, 1966, McGhee 1999). 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 (Okamoto 1988, Vermeij 1993, Savazzi 1996, McGhee 1999, Chirat et al. 2021, Ohta et al. 2025).

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. 1A,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. 1A,B). The isometrically growing conical shell (Thompson [1942] 1992, Raup 1966) is a special case, where the allometric relation $z(r)$ reduces to simple proportionality. The constant T, then, becomes Raup's dimensionless *translation* parameter (Raup 1966), related to β, the half-apical angle (hereafter, *apical angle*; $T = \cot\beta$; Fig. 1B).

A shell, however, is not a single helicospiral, but a three-dimensional structure made of "a bunch" of such spirals — hereafter, *multispiral* approach (Fig. 1D; also called multivector; Thompson [1942] 1992, Bayer 1978, McGhee 1999). Alternatively, a shell can be described

by a *generating curve*, a closed figure that sweeps through space along a logspiral *centerline* (Fig. 1C) (Thompson [1942] 1992, Raup 1961, 1966). These logspirals share a single common value of expansion rate (Illert 1983) — α in Eq.[1], or Raup's *whorl expansion rate*, $W = e^{2\pi\alpha}$ (Raup 1961, 1966). By geometric necessity, however, they differ in other parameters (Bayer 1978). Particularly, in apical angle, β, and in the downward *lead angle*, γ (Fig. 1B,D,F,G; the term lead angle is adopted from mechanical engineering and manufacturing, where it denotes the angle of helical threads on a screw). Expansion rate, α, is typically small (< 0.2) in gastropods (Thompson [1942] 1992, Cameron 1981), 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" (Thompson [1942] 1992). 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.

DRAFT

Methods

DATASETS. Data on coiling parameters was obtained from tables in Schindel (1990) and Dryad repositories of Collins et al. (2021b) and Noshita et al. (2012). The latter dataset is augmented with additional data from a later study (Araki & Noshita 2023). (Dryad datasets: Noshita et al. 2011 and Collins et al. 2021a.) Data from Schindel and from Noshita et al. contain together estimates of coiling parameters, such as whorl expansion rate (W) apical angle (T), or spire expansion rate (Schindel's M) for many specimens of marine, freshwater and terrestrial gastropod species. These parameter estimates can be transformed (see below) to the coiling parameters of this study (Eqs.[1] and [2]).

Collins et al. (2021b) provided a large dataset containing ontogenetic sequences of apertures of fossil and recent marine gastropods, obtained from sectioned specimens or microtomography. Their dataset contains both images of sectioned specimens and morphometric measurements of coiling axes, aperture areas, aperture centroids, etc. (Fig. 2C). This dataset, therefore, provides an opportunity to directly estimate spiral centerlines (Fig. 1C), their potential allometry, and the adequacy of the conical logspiral model.

DATA TRANSFORMATION AND REANALYSIS. Values of W and M from Schindel (1990) were transformed to α and k of this study by $\alpha = \frac{\log W}{2\pi}$ and $k = \frac{\log M}{\log W}$, respectively. For data from Noshita et al. (2012), W was similarly transformed to α, and values of T were transformed to apical angles of centerline spirals through $\cot\beta = 2T$. (More detail in 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, thus, correcting measured z-coordinates of centroids accordingly (Fig. 2C). Per-specimen coiling and allometry parameters were obtained by linear regression or by principal component analysis. Inter-clade differences and individual variability in growth and allometry were estimated with mixed-effect linear growth models (Grimm et al. 2017).

Overall, I investigated the growth and allometry of (*i*) centerline spirals, $r(\theta)$, from which α is estimated; (*ii*) spire height, $z(r)$, from which k and $\cot\beta$ can be estimated; (*iii*) aperture

area, $A(r)$ (A denoting aperture area), to compare with previous studies on aperture allometry; and (*iv*) spire height against cumulative centerline spiral length (i.e., arc length, denoted by s), $z(s)$, from which the lead angle, $\tan\gamma$, can be estimated. As part of the reanalysis, I also generated `svg` images (e.g., Fig. 2C) from the original `jpg` files in the dataset, for convenient visual inspection of fitted conical logspiral models. (More detail in SI.)

For all specimens, from all datasets, additional data, such as species, genus, family, specimen ID, scales of images, etc. were compiled.

DRAFT

Results and Discussion

Schindel (1990) 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 (Klingenberg 1996), though he did not make 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. 2A 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* ($k > 1$; Vermeij 1980).

More recently, Collins et al. (2021b) provided a larger dataset containing ontogenetic 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. 2C; SI). Centerline spirals follow the isometric conical logspiral model more tightly than in Schindel's data (Fig. 2B; 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 2.11 [2.073, 2.145], for *Maoricolpus*, 1.66 [1.59, 1.73] for *Tylospira* clade and 1.876 [1.845, 1.905] for rest of Struthiolariidae. Estimated within-clade standard deviation in allometric exponent among specimens is 0.0876 [0.0607, 0.1108], much lower than the inter-clade differences. The effect, in either direction, however, 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. (2021).

Accordingly, *Maoricolpus* are high-spired, and within Struthiolariidae the *Tylospira* clade is relatively low-spired (Fig. 2D). I note that these values for aperture allometry are in rough agreement with previously published estimates, obtained by regressing aperture area on body weight for land snail species (Cameron 1981). Differences in study organisms and methodology and comparison to theory merit further investigation.

Observed covariation in coiling parameters and uneven distribution in morphospace often receive adaptationist interpretations, such as mechanical strength, postural stability or economical shell construction (Raup 1966, Noshita et al. 2012, Okabe & Yoshimura 2017, Páll-Gergely et al. 2024). 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 (1966) 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. 2D; SI). Similar conditions can be formulated for non-circular apertures (Fig. 2D; 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. 2E shows estimates of lead angle for the dataset of Collins et al. 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 expanding aperture, providing a way for "moving the β parameter down to the mantle edge" (Løvtrup & Løvtrup 1988). Furthermore, adopting α and γ as the natural axes of coiling behavior is strongly supported by experiments and observations on within-species developmental plasticity (e.g., scalariforms or "corkscrew"s) and effects of variation in soft-body growth on shell morphology (Vermeij 1980, 1993, Kemp & Bertness 1984, Checa et al. 1998, Clewing et al. 2015).

Growth map models (Fig. 1E; SI; Rice 1998, Ubukata 2003, Hammer & Bucher 2005, Urdy et al. 2010) and the differential geometry tradition in theoretical morphology (Okamoto 1988, Noshita 2014, Chirat et al. 2021, Ohta et al. 2025; 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 (Okamoto 1988, Chirat et al. 2021, Ohta et al. 2025). Taking the multispiral standpoint, helicospirals on the shell (Fig. 1D), designated by position on the aperture, φ (Fig. 1F), differ in torsion-curvature ratios, which are another way to define $\tan\gamma$. For allometrically growing shells, torsion-curvature ratios also vary ontogenetically within each spiral. In terms of developmental plasticity, variation in curvature-torsion that anyhow occurs among helicospiral paths, also in the isometric case, is manifested within each such path in the allometric case.

A shell's aperture, therefore, dictates a gradient in lead angle (Fig. 1D,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 helicospiral paths on the shell's surface 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. 1D). But as the aperture begins to close, both factors in Eq.[3] become larger, resulting in increasing divergence of spiral paths in both abapical and adaxial direction (Fig. 1D,F). That is a direct geometric consequence of logspiral coiling. Rates and directions of cellular growth and division that are correlated with this gradient (Johnson et al. 2019, Ohta et al. 2025) are, therefore, a null expectation, for both isometric and allometric shell growth. In developmental plasticity parlance, whether the cellular processes are "leaders" or "followers" (West-Eberhard 2003) remains, however, to be determined. Moreover, previously formulated challenges to fine control of global shell form in gastropods by apertural growth rates still remain (Hutchinson 1990).

Overall, and in the manner of D'Arcy Thompson (Thompson [1942] 1992), 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 (van Osselaer & Grosjean 2000), 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. 2A,B; SI). This claim should be further scrutinized for terrestrial gastropods, as this study examined only marine species. More broadly, such geometric relationships are useful in defining natural axes of variation for data analyses and in combining data from several sources, obtained by different methodologies, as I have demonstrated here (Fig. 2B,D,E; SI). Adaptationist approaches should similarly acknowledge alternative, often indistinguishable, explanations that emerge from such "laws of form" (Fig. 2D,E). A final application is in addressing the enduring topic in paleobiology and evolutionary biology of interpreting spatiotemporal patterns of morphological diversity, in light of interchangeability of genetic and environmental influences (West-Eberhard 2003) and widely observed intraspecific plasticity in growth, development and morphology (Kemp & Bertness 1984, Arendt 1997, 2015, Checa et al. 1998, van der Sman et al. 2009, Clewing et al. 2015).

DRAFT

Acknowledgements

I thank Inon Scharf, Ofer Ovadia and Rodrigo B. Salvador for their time, patience and valuable comments on previous drafts of this report. I thank Cristian Seres for aid with verification of digitized datasets. Images in Fig. 1F,G from Raup (1961) and Johnson et al. (2019), reproduced here under fair use and conditions of the PNAS license. The original illustrations of *Ecphora* (Fig. 1F) are by John S. Spurbeck.

DRAFT

DATA AND SOFTWARE AVAILABILITY. All data, code and images (except original images for Fig. 1F,G) are available at https://doi.org/10.5281/zenodo.15723486. Web app for theoretical morphology of coiled shells (Fig. 1A,C-E) is available at https://doi.org/10.5281/zenodo.15518552.

References

Araki, A. & Noshita, K. 2023. Theoretical morphological analysis of differential morphospace occupation patterns for terrestrial and aquatic gastropods. *Evolution* **77**: 1864–1873. https://doi.org/10.1093/evolut/qpad110.

Arendt, J. 2015. Why get big in the cold? size–fecundity relationships explain the temperature-size rule in a pulmonate snail (*Physa*). *J. Evol. Biol.* **28**: 169–178.

Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* **72**: 149–177.

Bayer, U. 1978. Morphogenetic programs, instabilities, and evolution — a theoretical study. *Neues Jahrb. Geol. Paläont. Abh.* **156**: 226–261.

Cameron, R.A.D. 1981. Functional aspects of shell geometry in some british land snails. *Biol. J. Linn. Soc.* **16**: 157–167. https://doi.org/10.1111/j.1095-8312.1981.tb01648.x.

Checa, A.G., Jimenez-Jimenez, A.P. & Rivas, P. 1998. Regulation of spiral coiling in the terrestrial gastropod *Sphincterochila*: an experimental test of the road holding model. *J. Morphol.* **235**: 249–257.

Chirat, R., Goriely, A. & Moulton, D.E. 2021. The physical basis of mollusk shell chiral coiling. *Proc. Natl. Acad. Sci. U.S.A.* **118**. https://doi.org/10.1073/pnas.2109210118.

Clewing, C., Riedel, F., Wilke, T. & Albrecht, C. 2015. Ecophenotypic plasticity leads to extraordinary gastropod shells found on the ”roof of the world”. *Ecol. Evol.* **5**: 2966–2979. https://europepmc.org/articles/PMC4541999.

Collins, K.S., Klapaukh, R., Crampton, J.S., Gazley, M.F., Schipper, C., Maksimenko, A. &

Hines, B.R. 2021a. Data associated with: Going round the twist — an empirical analysis of shell coiling in helicospiral gastropods. Dryad Dataset. https://doi.org/10.5061/dryad.p5hqbzknw.

Collins, K.S., Klapaukh, R., Crampton, J.S., Gazley, M.F., Schipper, C., Maksimenko, A. & Hines, B.R. 2021b. Going round the twist—an empirical analysis of shell coiling in helicospiral gastropods. *Paleobiology* **47**: 648–665. https://doi.org/10.1017/pab.2021.8.

Edie, S.M., Collins, K.S. & Jablonski, D. 2024. Testing for allocation strategies and evolutionary tradeoffs in the bivalve shell. *J. Molluscan Stud.* **90**: eyae047. https://doi.org/10.1093/mollus/eyae047.

Grimm, K.J., Ram, N. & Eastabrook, R. 2017. *Growth Modeling: Structural Equation and Multilevel Modeling Approaches*. Guilford Press, New York.

Hammer, Ø. 2016. *Perfect Shape: Spiral Stories*. Springer.

Hammer, Ø. & Bucher, H. 2005. Models for the morphogenesis of the molluscan shell. *Lethaia.* **38**: 111–122.

Hutchinson, J.M.C. 1990. Control of gastropod shell form via aperture growth rates. *J. Morphol.* **206**: 259–264.

Illert, C. 1983. The mathematics of gnomonic seashells. *Math. Biosci.* **63**: 21–56.

Johnson, A.B., Fogel, N.S. & Lambert, J.D. 2019. Growth and morphogenesis of the gastropod shell. *Proc. Natl. Acad. Sci. U.S.A.* **116**: 6878 – 6883. https://doi.org/10.1073/pnas.1816089116.

Kemp, P. & Bertness, M.D. 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proc. Natl. Acad. Sci. U.S.A.* **81**: 811–813. https://doi.org/10.1073/pnas.81.3.811.

Klingenberg, C.P. 1996. Multivariate allometry. In: *Advances in Morphometrics* (L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor & D.E. Slice, eds), vol. 284 of *NATO Advanced Science Institutes Series*, pp. 23–49. Plenum Press, New York.

Løvtrup, S. & Løvtrup, M. 1988. The morphogenesis of molluscan shells: a mathematical account using biological parameters. *J. Morphol.* **197**: 53–62.

McGhee, G.R. 1999. *Theoretical Morphology : The Concept and Its Applications*. Perspectives in Earth History and Paleobiology. Columbia University Press, New York.

Moseley, H. 1838. On the geometrical forms of turbinated and discoid shells. *Philosophical Transactions of the Royal Society of London* **1838**: 351–370.

Moseley, H. 1842. On conchyliometry. *Lond. Edinb. Dubl. Phil. Mag.* **21**: 300–305.

Noshita, K. 2014. Quantification and geometric analysis of coiling patterns in gastropod shells based on 3d and 2d image data. *J. Theor. Biol.* **363**: 93–104.

Noshita, K., Asami, T. & Ubukata, T. 2011. Data from: Functional constraints on coiling geometry and aperture inclination in gastropods. Dryad Dataset. https://doi.org/10.5061/dryad.6mk023c0.

Noshita, K., Asami, T. & Ubukata, T. 2012. Functional constraints on coiling geometry and aperture inclination in gastropods. *Paleobiology* **38**: 322–334. 10.1666/10060.1.

Ohta, S., Noshita, K., Kimoto, K., Ishikawa, A., Sato, H., Shimizu, K. & Endo, K. 2025. Wnt activation causes shell malformation in lymnaeoidean gastropods. *J. Molluscan Stud.* **91**: eyaf001. https://doi.org/10.1093/mollus/eyaf001.

Okabe, T. & Yoshimura, J. 2017. Optimal designs of mollusk shells from bivalves to snails. *Scientific Reports* **7**: 42445. https://doi.org/10.1038/srep42445.

Okamoto, T. 1988. Analysis of heteromorph ammonoids by differential geometry. *Paleobiology* **31**: 35–52.

Páll-Gergely, B., Sipos, A.Á., Harzhauser, M., Örstan, A., Winkler, V. & Neubauer, T.A. 2024. Many roads to success: alternative routes to building an economic shell in land snails. *Evolution* **78**: 778–786. https://doi.org/10.1093/evolut/qpae018.

Raup, D.M. 1961. The geometry of coiling in gastropods. *Proc. Natl. Acad. Sci. U.S.A.* **47**: 602–609. https://doi.org/10.1073/pnas.47.4.602.

Raup, D.M. 1966. Geometric analysis of shell coiling: general problems. *J. Paleontol.* **40**:

1178–1190.

Rice, S.H. 1998. The bio-geometry of mollusc shells. *Paleobiology* **24**: 133–149.

Savazzi, E. 1990. Biological aspects of theoretical shell morphology. *Lethaia.* **23**: 195–212.

Savazzi, E. 1996. Adaptaions of vermetid and siliquarid gastropods. *Palaeontology* **39**: 157–177.

Schindel, D.E. 1990. Unoccupied morphospace and the coiled geometry of gastropods: architectural constraint or geometric covariation? In: *Causes of Evolution: a paleontological perspective* (R. Ross & W. Allmon, eds), pp. 270–304. University of Chicago Press, Chicago.

Seilacher, A. 1973. Fabricational noise in adaptive morphology. *Syst. Biol.* **22**: 451–465. https://doi.org/10.2307/2412952.

Stone, J.R. 1996. The evolution of ideas: a phylogeny of shell models. *Am. Nat.* **148**: 904–929.

Thompson, D.W. [1942] 1992. *On Growth and Form: The Complete Revised Edition*. Dover, New York.

Ubukata, T. 2003. Pattern of growth rate around aperture and shell form in bivalvia: a theoretical morphological study. *Paleobiology* **29**: 480–491.

Urdy, S. 2015. Theoretical modelling of the molluscan shell: What has been learned from the comparison among molluscan taxa? In: *Ammonoid Paleobiology: From anatomy to ecology* (C. Klug, D. Korn, K. De Baets, I. Kruta & R.H. Mapes, eds), pp. 207–251. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-017-9630-9_6.

Urdy, S., Goudemand, N., Bucher, H. & Chirat, R. 2010. Allometries and the morphogenesis of the molluscan shell: a quantitative and theoretical model. *J. Exp. Zool.* **314B**: 280–302. 10.1002/jez.b.21337.

van der Sman, J., Phillips, N.E. & Pfister, C.A. 2009. Relative effects of maternal and juvenile food availability for a marine snail. *Ecology* **90**: 3119–3125.

van Osselaer, C. & Grosjean, P. 2000. Suture and location of the coiling axis in gastropod shells. *Paleobiology* **26**: 238–257. https:

//doi.org/10.1666/0094-8373(2000)026<0238:SALOTC>2.0.CO;2.

Vermeij, G.J. 1980. Gastropod shell growth rate, allometry, and adult size. In: *Skeletal Growth of Aquatic Organisms* (D. Rhoads & R. Lutz, eds), pp. 379–393. Plenum Press, New York.

Vermeij, G.J. 1993. *A Natural History of Shells*. Princeton University Press, Princeton, Oxford.

West-Eberhard, M.J. 2003. *Developmental plasticity and evolution*. Oxford University Press, New York.

DRAFT

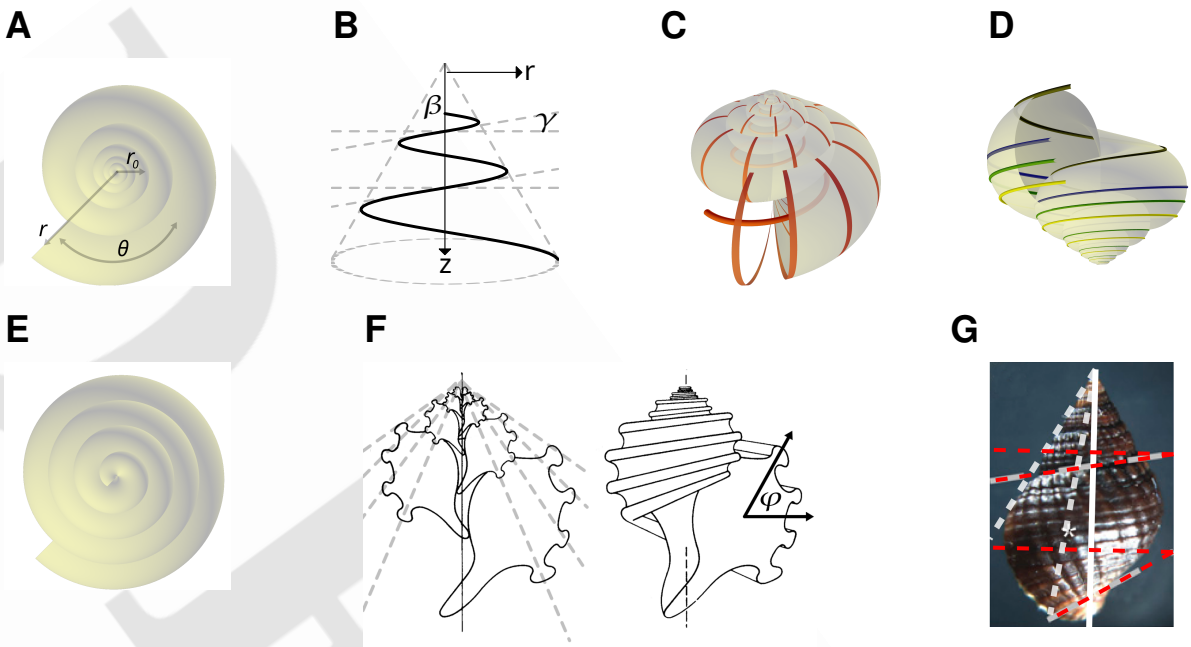

Figure 1 : Theoretical morphology in a snailshell. (***A***) Logspiral shell in apical view. Radius, r, revolution angle, θ, and initial size, $r_0 = r(\theta = 0)$, are illustrated. (***B***) Conical logspiral in lateral view. (Half-)Apical angle, β, and lead angle, γ, are defined. (***C***) Generating 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 (Raup 1961). 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. (2019). 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.

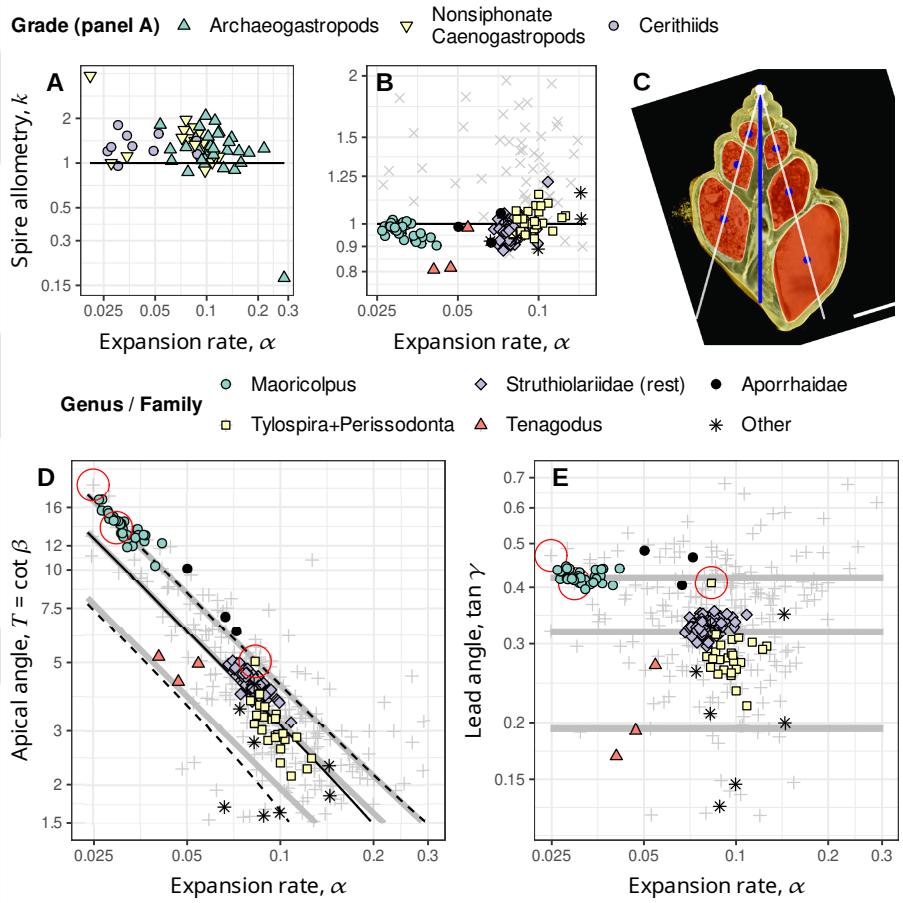

Figure 2 : Empirical covariation of coiling parameters. (***A***) Spire allometry, k, for Schindel's (1990) gastropod taxa, divided among his three "grades". With the notable, but unsurprising, exceptions of *Haliotis* and *Truncatella*, scatter does not deviate much from isometry ($k = 1$; solid black). Deviations are biased upwards, towards doming. (***B***) Same for the reanalyzed data of Collins et al. (2021b). 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 (2012) survey of coiling parameters is also presented (gray), where values of $\cot\beta$ were converted to represent centerlines (Methods; 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 (1966) 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, 0.425), for *Maoricolpus*, 0.281 (0.267, 0.294) for *Tylospira* clade and 0.325 (0.322, 0.327) for rest of Struthiolariidae.