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Author for correspondence:
Katie S. Collins
e-mail: k.collins@nhm.ac.uk

† These authors contributed equally and are joint first authors on this work.

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Convergence and contingency in the evolution of a specialized mode of life: multiple origins and high disparity of rock-boring bivalves

Katie S. Collins[1,†], Stewart M. Edie[2,†] and David Jablonski[3]

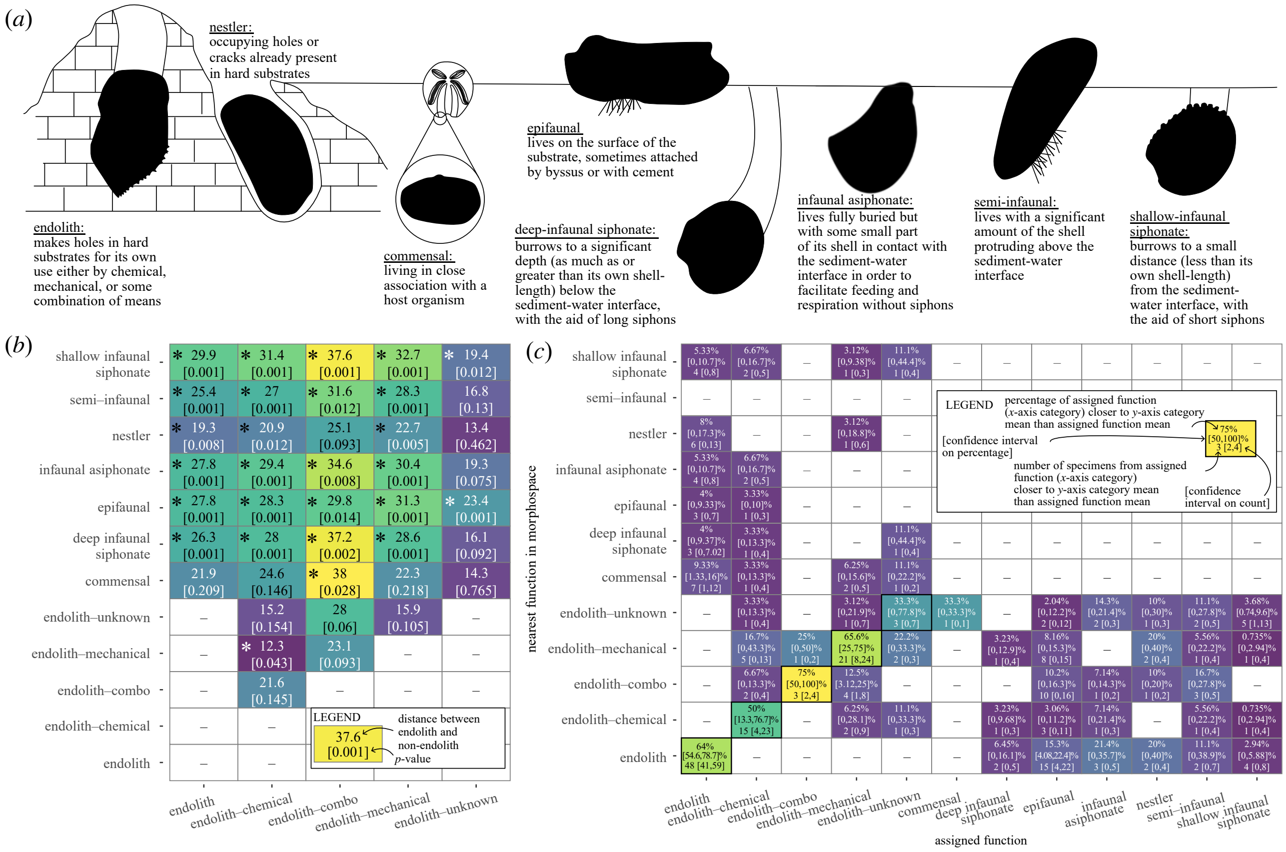
[1]The Natural History Museum, Cromwell Road SW7 5BD, London, UK
[2]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA
[3]Department of the Geophysical Sciences, University of Chicago, Chicago, IL 60637, USA

KSC, 0000-0002-3379-4201; SME, 0000-0003-2843-7952

Evolutionary adaptation to novel, specialized modes of life is often associated with a close mapping of form to the new function, resulting in narrow morphological disparity. For bivalve molluscs, endolithy (rock-boring) has biomechanical requirements thought to diverge strongly from those of ancestral functions. However, endolithy in bivalves has originated at least eight times. Three-dimensional morphometric data representing 75 species from approximately 94% of extant endolithic genera and families, along with 310 non-endolithic species in those families, show that endolithy is evolutionarily accessible from many different morphological starting points. Although some endoliths appear to converge on certain shell morphologies, the range of endolith shell form is as broad as that belonging to any other bivalve substrate use. Nevertheless, endolithy is a taxon-poor function in Bivalvia today. This limited richness does not derive from origination within source clades having significantly low origination or high extinction rates, and today's endoliths are not confined to low-diversity biogeographic regions. Instead, endolithy may be limited by habitat availability. Both determinism (as reflected by convergence among distantly related taxa) and contingency (as reflected by the endoliths that remain close to the disparate morphologies of their source clades) underlie the occupation of endolith morphospace.

1. Introduction

The evolutionary invasion of a novel adaptive zone [1] or functional group [2] by multiple lineages can be viewed in terms of two end-member scenarios. In one, transitions toward an unusual mode of life for the ancestral clade (as functional specialization) may be accompanied by a narrowing of suitable morphologies [3–7]. This is the familiar scenario for fast-swimming aquatic predators such as dolphins, ichthyosaurs and tuna, which involved deterministic convergence on a single ecomorphic design [5,8,9], with many more examples across the tree of life. Less frequently reported is the scenario involving more contingent transitions to a given function by disparate clades without marked convergence, such as insectivores that extract prey from tree bark including woodpeckers and certain species of Galapagos finches, lemurs, opossums and Hawaiian honeycreepers [9,10]. Here, we investigate which scenario best describes a remarkable polyphyletic functional adaptation in marine bivalves: boring into hard substrata (endolithy). This seemingly demanding and specialized transition, entailing an ability to penetrate substrata that may be harder than the shell of the borers—including basalt, andesite, gneiss and marine plastics [11–15]—might be expected to follow the dolphin scenario, converging on a single adaptive peak representing an optimized biomechanical solution. Here



	endolith	endolith–chemical	endolith–combo	endolith–mechanical	endolith–unknown
shallow infaunal siphonate	* 29.9 [0.001]	* 31.4 [0.001]	* 37.6 [0.001]	* 32.7 [0.001]	* 19.4 [0.012]
semi–infaunal	* 25.4 [0.001]	* 27 [0.001]	* 31.6 [0.012]	* 28.3 [0.001]	16.8 [0.13]
nestler	* 19.3 [0.008]	* 20.9 [0.012]	25.1 [0.093]	* 22.7 [0.005]	13.4 [0.462]
infaunal asiphonate	* 27.8 [0.001]	* 29.4 [0.001]	* 34.6 [0.008]	* 30.4 [0.001]	19.3 [0.075]
epifaunal	* 27.8 [0.001]	* 28.3 [0.001]	* 29.8 [0.014]	* 31.3 [0.001]	* 23.4 [0.001]
deep infaunal siphonate	* 26.3 [0.001]	* 28 [0.001]	* 37.2 [0.002]	* 28.6 [0.001]	16.1 [0.092]
commensal	21.9 [0.209]	24.6 [0.146]	* 38 [0.028]	22.3 [0.218]	14.3 [0.765]
endolith–unknown	–	15.2 [0.154]	28 [0.06]	15.9 [0.105]	–
endolith–mechanical	–	* 12.3 [0.043]	23.1 [0.093]	–	–
endolith–combo	–	21.6 [0.145]	–	–	–
endolith–chemical	–	–			
endolith	–	–			

Figure 1. Definitions of ecologic functions and the distinctiveness of endolith morphologies within families. (*a*) Cartoon illustrations and explanations of different substratum uses. Silhouettes are not to scale and do not represent specific specimens or taxa included in the analysis, they are for illustrative purposes only. (*b*) Differences between means for endolith morphology and for other substratum uses (light colours indicate larger differences, dark colours indicate smaller differences, asterisks indicate significantly different means, '–' indicates pairs not compared). (*c*) Proportion and counts of taxa for one functional group (*x*-axis category) that lie closer to the mean of another functional group (*y*-axis category). Diagonals (indicated by hard black borders) give the coherence (see text) for each group (i.e. how many taxa lie closest to their group mean). Off-diagonals give the encroachment (see text) of the *x*-axis category upon the *y*-axis category (i.e. 20% of nestlers encroach upon mechanical endolith morphospace; 16.7% of chemical endoliths encroach upon mechanical endolith morphospace).

we test these deterministic and contingent scenarios in the first high-resolution three-dimensional morphometric examination of this bivalve functional group.

Endolithic bivalve taxa either bore directly into a rock or modify existing cracks or boreholes via mechanical rasping by their shell valves [16,17] and/or production of calcium-binding mucoproteins [18–21]. If this function is under selection for efficient substratum penetration, potentially driven by predation pressure [22,23], then either of these excavation methods should select for streamlined, narrow shell profiles in the direction of boring, as is observed for bivalve taxa that burrow into sand and mud [24,25] (figure 1*a*). Boring may also select for more elongate shells, as is hypothesized for the boring mytilids *Lithophaga* and *Botula* [26]. The additional challenge of excavating substrata of equivalent or greater material hardness may select for shapes that promote penetrative abilities while resisting critical damage to the bivalve's shell [23], including aspects of the shell sculpture as hypothesized for boring mytilids and pholads [11,18,27].

Endolithy is necessarily limited to places where appropriate hard substrata are available, which may ultimately affect the origination and modern geographical distribution of endoliths. While we do not yet have a clear and comprehensive picture of global benthic habitats [28], the seafloor is certainly not homogeneous: hardgrounds are not available to the same extent everywhere regardless of geography or depth (e.g. [29]), and given that many endoliths are specifically associated with coral substrata [23,30], the origination and distribution of corals could strongly affect the biogeography of endoliths. Given this potential limitation in suitable habitat, endolith macroevolution may be highly probabilistic, meaning it is most likely to originate in clades with more global distributions, high taxon production and low taxon extinction (i.e. a 'supply-side' dynamic) [31,32].

We expect that the apparently unique functional demands of endolithy will result in (1) shell shapes distinct from those associated with other functions (figure 1*b*,*c*) regardless of boring method, and (2) reduced overall disparity of shell shapes among phylogenetically distant groups of endoliths (endolithy has long been known to be polyphyletic). We also analyse the diversification history of lineages containing endoliths at a larger scale to test two null hypotheses, that: (1) all else being equal, endolithy is most likely to evolve in clades with the highest rates of genus origination or lowest extinction; and (2) endolith richness patterns will coincide biogeographically with those shown by the class as a whole. In combination, these analyses can address one of the fundamental questions in biology, the roles of determinism and contingency in driving the evolution of biological form.

2. Material and methods

(a) Taxonomic and specimen sampling

Marine Bivalvia contains 211 extant endolithic species in 52 genera and 8 families (database of [31,32], new version as electronic supplementary material, dataset S1, frozen 12 February 2021). Species that are known to actively modify pre-existing cavities, a subset of the taxa classed as nestlers (bivalves which occupy already-existing cracks or cavities), are included here as endoliths, e.g. *Pedum spondyloideum*. Sampled endolithic specimens were further designated as mechanical, chemical, or combination borers using primary literature (electronic supplementary material, dataset S1). Although authors (e.g. [17]) have asserted that many taxa may employ a combination of boring methods, the Gastrochaenidae were the only taxon we could find with direct assertion of combination boring (in [33]). The Pholadidae are entirely endolithic, and so were operationally combined for specified analyses with their close relatives, the mostly non-endolithic Myidae. Three other families containing endoliths were omitted: shells of the Clavagellidae are so highly modified that they could not be included in this morphometric scheme; we were unable to access a specimen of the sole endolithic teredinid *Lithoredo* [34]; and the stiff-sediment borers in the freshwater unionoid family Mycetopodidae [35] were omitted from quantitative analyses but are considered in the Discussion. Hypothesized phylogenetic relationships of bivalve families are from [36] and references therein, totaling 97 families.

For morphological analyses, one shell valve from an adult individual (i.e. adult size range reported in the literature) was sampled from museum collections for 49 of the 52 endolithic genera (totaling 74 extant species and 1 extinct species), and for 307 of the 328 remaining non-endolithic genera from those same families (328 species; electronic supplementary material, dataset S1). Left valves were sampled for all inequivalve taxa; for equivalve taxa, if no left valve was available, a right valve was sampled and digitally mirrored about the commissure to serve as a left valve (see [37] for determining valve handedness). Two-dimensional images of seven fossil taxa representing the earliest known members of clades containing endoliths were used to qualitatively compare the similarity of ancestral and extant endolithic morphologies.

(b) Quantitative characterization of shell morphology

Specimens were scanned using micro-computed X-ray tomography (µCT) at the University of Chicago Paleo-CT Facility and the National Museum of Natural History Scientific Imaging Facility. Three-dimensional, isosurface, triangular-mesh models were created in VG Studio Max and ORS Dragonfly, then made manifold and watertight using cleaning routines in Rvcg [38] and Meshmixer. All meshes are available online via links in electronic supplementary material, dataset S1.

The shape of the shell valve's exterior surface (i.e. the side facing the ambient environment) was extracted and aligned for comparative morphometrics using the procedure from [39]—briefly summarized here with full details in electronic supplementary material, §S2. The hinge line was landmarked using the two farthest-apart articulating elements of the hinge area. A curve of sliding semilandmarks was placed on the shell commissure ($n = 50$), and a grid of sliding semilandmarks was placed on the shell's exterior surface ($n = 289$). Semilandmark density was determined using the Landmark Sampling Evaluation Curve [40] (electronic supplementary material, figure S1). Semilandmarks were then aligned by minimizing the sum-of-squares distances between the standardized anatomical axes of shells (i.e. the hinge line, orthogonal hinge line, and sagittal axis; electronic supplementary material, figure S2). The dimensionality of these aligned semilandmark configurations were reduced using principal components analysis (PCA; electronic supplementary material, figure S3 and §S3). A plot of disparate shell shapes across the PC axes suggests that most shape variation is captured by PCs 1–18, which explain 95% of the total variance (electronic supplementary material, figure S4). Thus, PCs 1–18 were used for analyses of shell shape.

(c) Distinctiveness of endolithic shell shape

The difference in mean shape of the endolithic habit from that of all other substratum uses was tested via a residual randomization permutation procedure (999 permutations using *RRPP::pairwise* [41]) on a linear model of PC scores to substratum uses (i.e. PCs 1:18; *RRPP::lm.rrpp*). Because mean shapes are often significantly different, even with broad overlap of specimens between *a priori* groups in morphospace, the coherence of endolithy was calculated as the proportion of its genera closest to its mean shape. The incoherence of endolithy was expressed as the proportion of its genera closest to the mean shape of non-endolithic substratum uses. Encroachment on the endolithic morphospace was calculated as the proportion of genera from non-endolithic substratum uses that were closer to the endolithic mean shape than their own. Uncertainty was calculated across 999 bootstrapped distributions of members within substratum uses. This approach provides an additional indication of how endolithy is dispersed through the morphospace.

(d) Disparity of endolithic shell shape

Shell disparity among substratum uses was measured in two ways: (1) as the Procrustes variance of the aligned semilandmarks centered on group means (*sensu* [42]; see *geomorph::morphol.disparity* [43]), and (2) as the cumulative sum of PC ranges (e.g. [44]; see electronic supplementary material, §S4). Uncertainty for both measures of disparity was estimated by bootstrapping specimens within groups (e.g. substratum uses), and confidence intervals were taken as the upper and lower bounds of the inner 95% quantile of resampled disparity values. Confidence intervals can be asymmetric about the observed value given that disparity must be positive; for cumulative range, the upper quantile cannot exceed the observed value and will often fall below it, reflecting the sensitivity of absolute morphospace breadth to sampling extreme values (further details in electronic supplementary material, §S4.2).

(e) Hypothesizing convergence of endolithic shell shape

The effect sizes of family membership and substratum uses were tested using an analysis of variance (ANOVA), as implemented by RRPP on a linear model of PC scores as a function of the interaction between family membership with substratum uses; the ANOVA was repeated for a binary classification scheme of substratum uses: endolithic versus non-endolithic uses (electronic supplementary material, §S4.3).

To hypothesize regions in morphospace where convergence or parallel evolution may have occurred (i.e. polyphyletic occupation of endolithic morphospace), the similarity of shell shape among endoliths in different families was analysed in a phylogenetic context. We use convergence and parallelism in the broad, phenotypic sense; convergence occurs when lineages starting at disparate points in morphospace evolve to become more similar, and parallel evolution occurs when similar forms, often closely related, traverse morphospace to similar evolutionary endpoints. In a multi-level approach, convergence might involve different developmental pathways to a similar endpoint, and parallelism repeated use of the same pathway [45,46], but changes at this level are not accessible for most organisms, living or fossil, and either pathway can underlie either phenotypic pattern [47]. Adding more fossil-derived ancestral morphologies and resolving lower-level phylogenetic relationships will also be necessary to formally differentiate morphological convergence from parallelism among endoliths (e.g. [46]), but the steps taken here provide expectations for focusing those efforts. Pairwise Euclidean distances were calculated between endolith shell shapes for taxa among families, which were then grouped by successively larger thresholds set by quantiles of all pairwise distances (i.e. those distances between 0–5%, –15%, –25%, –50%, –75%, –

100%). This approach measures similarity in a relative sense; it depends on the observed distribution of morphologies, which may not be similar in an absolute sense. Therefore, as a reference to the absolute similarity between shell shapes, the morphologies of maximally distant inter-family taxon pairs per threshold were visually compared. Using this approach, the 5%, 10% and 25% distance similarity thresholds were used when calculating the numbers of taxa with similar morphology between families (electronic supplementary material, figure S5).

(f) Diversification dynamics and biogeography of endolithy

Origination and extinction rates of genera in extant bivalve families were determined by the 'boundary-crossing, *per-capita*' method [48], drawn from a taxonomically and stratigraphically updated Phanerozoic database of first and last occurrences of fossil bivalve genera [49]; new version as electronic supplementary material, dataset S1, frozen 3 September 2022). Differences in median evolutionary rates were tested using a Mann–Whitney test. Spatial richness of endolithic species was expressed as the intersection of species' biogeographic ranges with a 50 × 50 km equal-area grid of the continental shelf (data from a taxonomically and geographically updated dataset of bivalve occurrences [32], new version as electronic supplementary material, dataset S1).

3. Results

(a) Indistinct and disparate endolithic morphologies

Endoliths, either as an entire group or per subcategory (chemical/mechanical/combo/unknown), tend to have significantly different mean shapes to other functions (figure 1*b*). Only the chemical and mechanical endoliths differ significantly among subcategories at $p = 0.05$, although the distance between their means is much smaller than most distances between endolithic to non-endolithic functions, suggesting that endoliths still have fairly similar shapes relative to other functions. Endoliths are generally over 50% coherent, and 'combo' endoliths are 75% coherent, although the small sample size ($n = 4$) and taxonomic constraints (only gastrochaenids are assigned 'combo') should be noted (see diagonal cells in figure 1). Around 36% of endoliths have shapes that lie closer to the mean shapes of non-endolithic functions, particularly chemical borers (cells above the diagonal in figure 1*c*). Genera from non-endolithic functions also encroach on the endolithic morphospace (cells below the diagonal in figure 1*c*, and see overlap in figure 2).

Because of this degree of overlap between areas of morphospace, the morphological disparity of endolithic taxa is among the highest of any habit (figure 2*c*). The two measures of disparity are largely congruent in their rank order, with notable deviations associated with larger sample sizes in epifaunal and shallow- and deep-infaunal siphonate groups (figure 2*c*). In effect, the distribution of endolithic shell morphologies appears to be multivariate leptokurtic, with many shapes concentrating in a certain region of morphospace and a wide but thin distribution of shapes towards the periphery of the morphospace. Endoliths account for greater proportions of a family's morphological disparity than its genus richness in all families except the Gastrochaenidae (e.g. only approx. 20% of venerids are endolithic, but those taxa contribute over 25% of the family's morphological variance; figure 2*d*).

(b) Polyphyly of endolithy

Endolithic species occur in 8 of the 97 extant bivalve families analysed here (figure 3*a*; 10 including Clavagellidae and Teredinidae, 11 including the freshwater Mycetopodidae). This limited phylogenetic diversity also manifests at the species level, where endolithic species compose only approximately 4% of extant marine bivalve species richness (211 of approx. 6000 species occurring at less than 200 m water depth [32]). The endolithic species are also distributed unevenly among those eight families, with 97% of richness concentrated in just four families: the strictly endolithic Pholadidae (with 76 spp), and the multi-functional Gastrochaenidae (27 spp), Veneridae (41 spp) and Mytilidae (61 spp). In the Mytilidae themselves, recent phylogenetic work (e.g. [54–56]) suggests that endolithy has arisen multiple times, with the subfamily Lithophaginae having been shown to be non-monophyletic (e.g. the distantly related *Lithophaga* and *Leiosolenus*, which were once considered congeners).

Family membership has a greater effect on the distinctiveness of shell shape than substratum use (electronic supplementary material, table S1a), and this ranking of effect sizes in the ANOVA holds when aggregating non-endolithic uses into a single category (electronic supplementary material, table S1b). Critically, shell shape depends more strongly on endolithic habit *and* family membership than on the endolithic habit alone (electronic supplementary material, table S1b), indicating that endoliths tend to have distinctive morphologies within their families but also that families themselves have distinctive morphologies; the relatively weak marginal effect of endolithy (electronic supplementary material, table S1b) is consistent with its overlap of shell shapes with other functions (figure 1*c*).

Nonetheless, certain endolithic species over five families occupy a confined region of morphospace (electronic supplementary material, figure S7), suggesting some degree of convergent evolution across a polyphyletic morphological continuum ranging from ultra-elongate and cylindrical (*Adula*, electronic supplementary material, figure S7) to subovate shells (*Platyodon*; electronic supplementary material, figure S7). Thus, there is no convergence on a singular shell shape, but instead on a collection of shapes within a subregion of bivalve morphospace. These similarly shaped endolithic taxa among families can approach 50% of the families' combined endolithic diversity (figure 3*b*). The convergences are not strictly among mechanical or chemical borers, with similar shapes arising between these endolithic modes (figure 3). Qualitatively, the elongate endoliths appear convergent relative to the oldest fossil members of their families (figure 3*a*, A versus F, J versus I, P versus R, and V versus Y). However, many other endoliths from these families, plus all species from two other families, fall outside this region of similar shell shapes (e.g. *Pedum* and *Fungiacava*; electronic supplementary material, figure S7).

(c) Evolutionary rates and geographical distribution of endolithy

Compared to families lacking endoliths, those containing endoliths do not have significantly different origination rates (figure 4*a*; Mann–Whitney $U = 277$, $p = 0.26$) or extinction rates (figure 4*b*, $U = 282$, $p = 0.79$). The earliest endoliths appear in the Late Ordovician, and other endolithic taxa

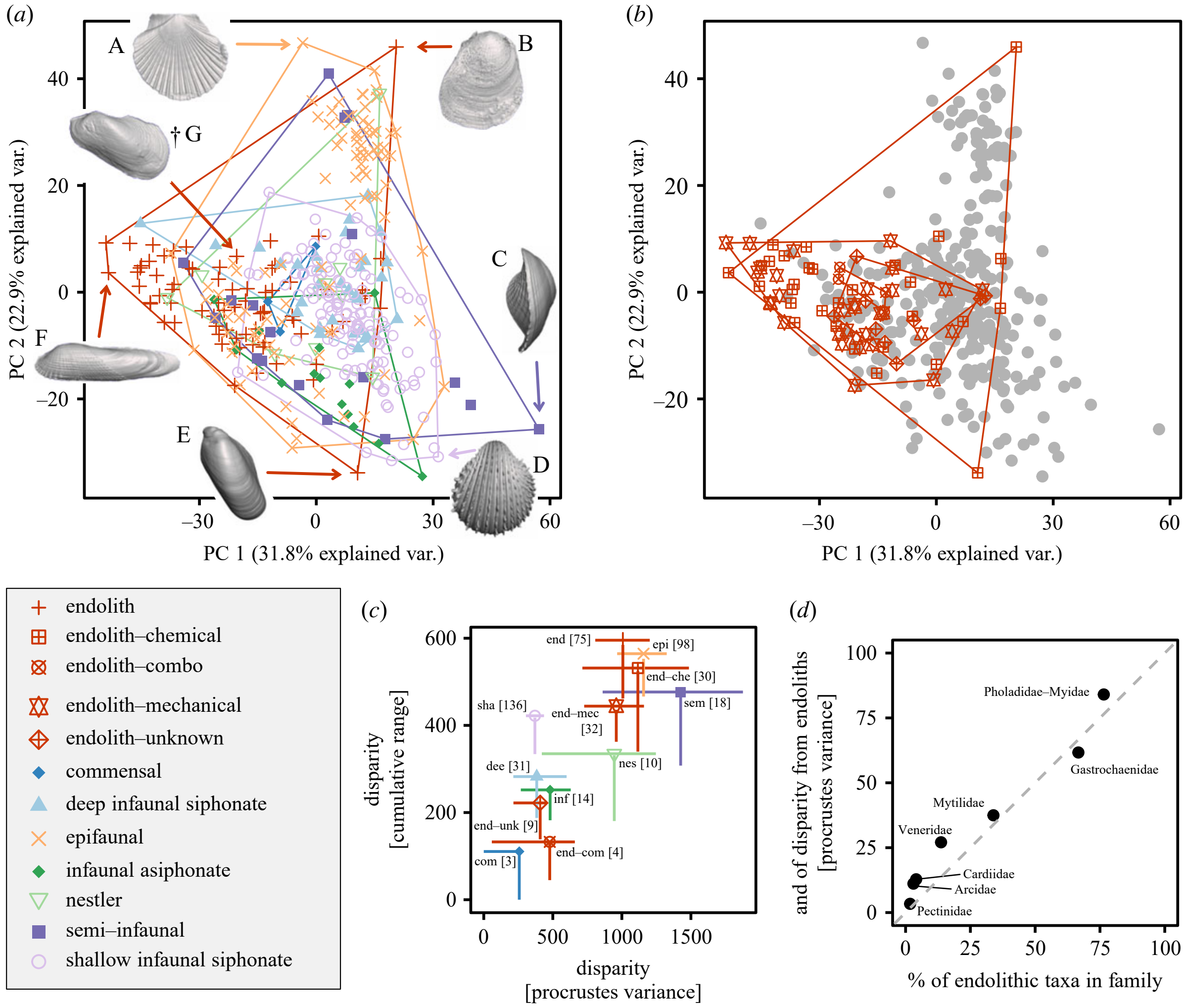


Figure 2. Primary axes of variation among taxa across substratum uses and their disparity. (*a*) Projections of genus morphology along the first two principal components, coloured by substratum use, with observed morphology of selected peripheral specimens. Figured taxa: **A** *Minnivola pyxidata* (Born, 1778) [Pectinidae], **B** *Pedum spondyloideum* (Gmelin, 1791) [Pectinidae], **C** *Corculum cardissa* (Linnaeus, 1758) [Cardiidae], **D** *Phlogocardia belcheri* (Broderip & Sowerby I, 1829) [Cardiidae], **E** *Fungiacava eilatensis* Soot-Ryen, 1969 [Mytilidae], **F** *Adula gruneri* (Philippi, 1851) [Mytilidae], **G** †*Corallidomus scobina* Pojeta & Palmer, 1976 [†Modiolopsidae]. (*b*) The same as in panel (*a*), but highlighting subcategories of endolithy. (*c*) Comparison of disparity values calculated by Procrustes variance and the cumulative range of PC scores. Points are observed values with 95% confidence intervals. (*d*) Proportion of disparity that endoliths contribute to the disparity of their family against the proportion of their diversity in the family. Dashed gray line shows the 1 : 1 relationship.

have arisen through the Mesozoic and Cenozoic, ranging from great antiquity (e.g. Gastrochaenidae) to relative youth (e.g. *Litharca*) and everything in between [23,30]. Biogeography of endolithic species richness follows that of the class, peaking in the tropics with a hotspot in the Indo-West Pacific (figure 4*c*).

4. Discussion

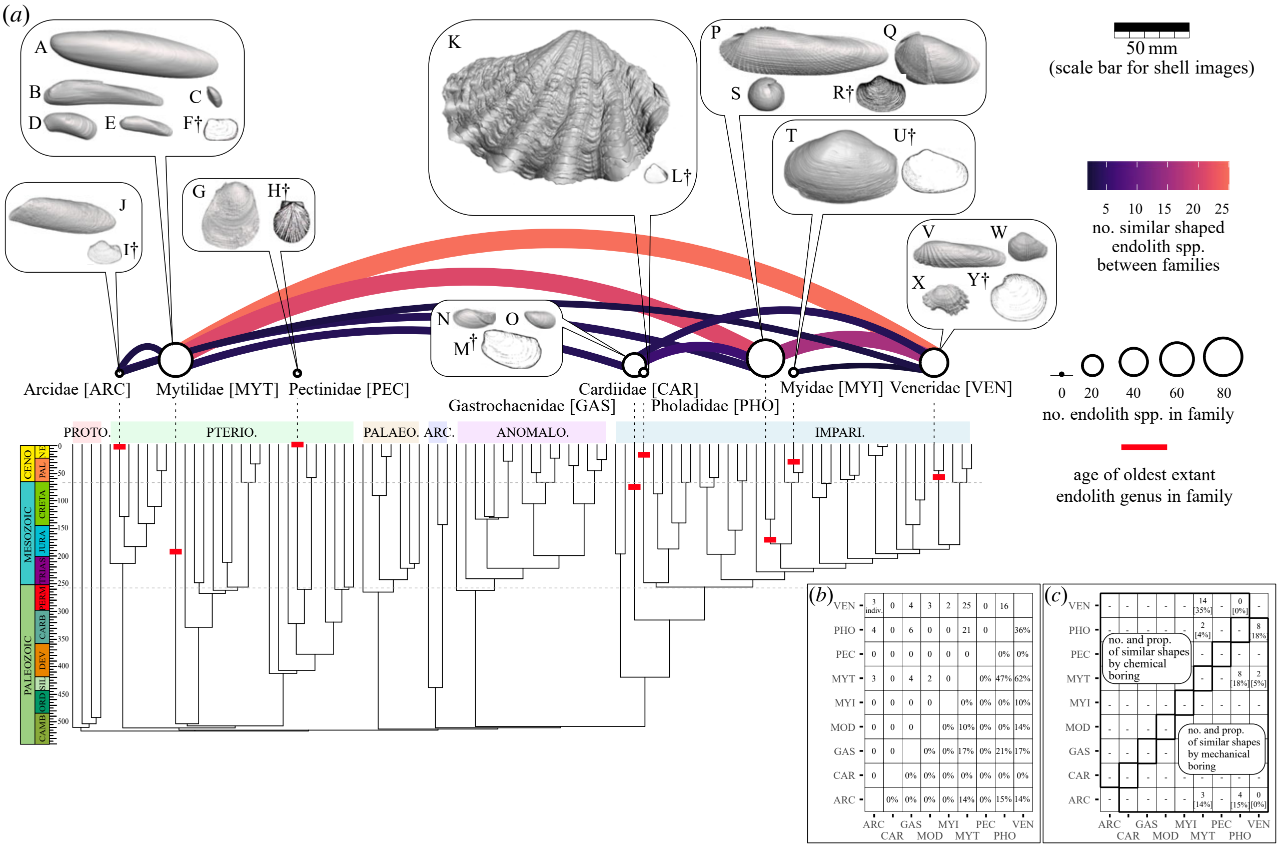
The bivalve shell is the animal's main interface with its physical and biological environment, and this often promotes close mapping between form and function with frequent convergences among distantly related clades [24,57,58]. However, despite the functional demands of the boring habit, endolithic shell morphology is not entirely distinct from those associated with other functions, and the disparity of the endolithic habit is as high or higher than that of any other substratum use. The subcategories of endolithy are also not strongly differentiated from each other in morphospace. This result parallels the results of Anderson [35], who found that ultra-elongate shells, such as those exhibited by some endoliths, occur in marine and freshwater bivalves occupying a variety of functions. Further, contrary to potential macroevolutionary and macroecological explanations for taxonomic richness, endoliths do not show exceptional or anomalous evolutionary rates or biogeographic patterns.

(a) Endolithy lacks a distinct morphology

Endolithy involves excavating substrata that can be at least as hard as the animal's calcium carbonate shell, which might be expected to impart a tight relationship between form and function. However, for the traits considered here, endolithy neither has lower disparity than other substratum uses, nor converges on a unique morphology. This fairly extreme functional transition evidently does not drive or require a shift to distinct and narrow morphologies.

(i) Alternative axes of morphological similarity?

The lack of a single endolithic morphology is unlikely to change with the inclusion of other traits thought to be related to endolithy. The relative length of the hinge—the region of the shell about which the valves rotate—has also been



(b)

	ARC	CAR	GAS	MOD	MYI	MYT	PEC	PHO	VEN
VEN	3 indiv.	0	4	3	2	25	0	16	
PHO	4	0	6	0	0	21	0		36%
PEC	0	0	0	0	0	0		0%	0%
MYT	3	0	4	2	0		0%	47%	62%
MYI	0	0	0	0		0%	0%	0%	10%
MOD	0	0	0		0%	10%	0%	0%	14%
GAS	0	0		0%	0%	17%	0%	21%	17%
CAR	0		0%	0%	0%	0%	0%	0%	0%
ARC		0%	0%	0%	0%	14%	0%	15%	14%

(c)

	ARC	CAR	GAS	MOD	MYI	MYT	PEC	PHO	VEN
VEN	-	-	-	-	-	14 [35%]	-	0 [0%]	-
PHO	-	-	-	-	-	2 [4%]	-	-	8 [18%]
PEC						-	-	-	-
MYT						-	-	8 [18%]	2 [5%]
MYI	-	-	-	-	-	-	-	-	-
MOD	-	-	-	-					
GAS	-	-	-	-					
CAR	-	-	-	-	-	-	-	-	-
ARC	-	-	-	-	-	3 [14%]	-	4 [15%]	0 [0%]

Figure 3. Phylogenetic distribution of endolithic species richness, shell shape convergence, and exemplar shell morphologies. (*a*) Curved lines connecting families indicate the number of similarly shaped taxa at the 5% distance threshold. Exemplar endolithic taxa, plus oldest fossil members of sampled families: **A** *Lithophaga teres* (Philippi, 1846), **B** *Adula gruneri* (Philippi, 1851), **C** *Fungiacava eilatensis* Soot-Ryen, 1969, **D** *Botula fusca* (Gmelin, 1791), **E** *Adula californiensis* (Philippi, 1847), **F** †*Phthonia regularis* (Barrande, 1881) after [50], **G** *Pedum spondyloideum* (Gmelin, 1791), **H** †*Avichlamys csopakensis* (Frech, 1905), **I** †*Eonavicula minuta* (J. de C. Sowerby, 1824) after [51]), **J** *Litharca lithodomus* (G. B. Sowerby I, 1833), **K** *Tridacna crocea* (Lamarck, 1819), **L** †*Protocardia contusa* Healey, 1908, **M** †*Kalentera riccardii* Damborenea, 2004, **N** *Spengleria rostrata* (Spengler, 1783), **O** *Gastrochaena cuneiformis* Spengler, 1783, **P** *Thovana campechiensis* (Gmelin, 1791), **Q** *Chaceia ovoidea* (Gould, 1851), **R** †*Antiqucorbula concentrica* after [52], **S** *Jouannetia cumingii* (G. B. Sowerby II, 1849), **T** *Platyodon cancellatus* (Conrad, 1837), **U** *Sphenia duponti* Cossmann, 1908, **V** *Petricolaria cognata* (C. B. Adams, 1852), **W** *Choristodon robustus* (G. B. Sowerby I, 1834), **X** *Asaphinoides madreporicus* (Jousseaume, 1895), **Y** †*Austrocardilanx antarctica* (Quilty, 1983) after [53]. The 50 mm scalebar applies to figures A-Y. Red bars on phylogeny indicate the geological age of the oldest extant endolith in the family (refer to geological timescale on left hand side). Coloured areas of the phylogeny indicate major bivalve clades: from left to right, Protobranchia (red), Pteriomorphia (green), Paleoheterodonta (yellow), Archiheterodonta (purple), Anomalodesmata (pink), Imparidentia (blue). (*b*) Counts of taxa in family pairs with distances less than the 5% threshold (upper left triangle), and the proportion of similar taxa across all endolithic taxa in family pairs (lower right triangle). Counts at higher thresholds in electronic supplementary material figure S6. (*c*) As for panel b, but cells above the diagonal give counts and percentages of chemically boring taxa that are similar in family pairs, cells below the diagonal record counts and percentages of mechanically boring taxa that are similar in family pairs.

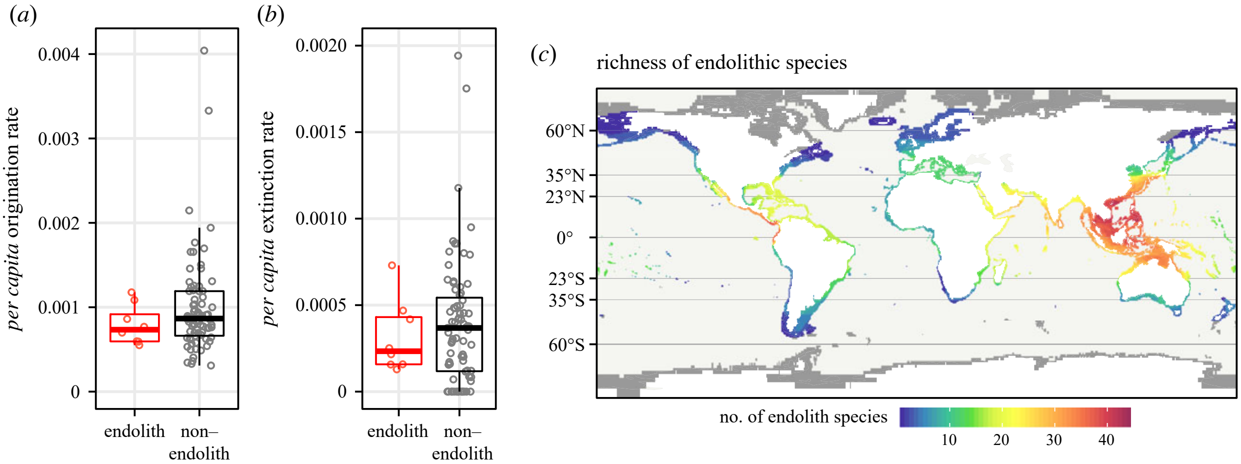


Figure 4. Evolutionary rates and geographical distribution of endolith lineages. (*a,b*) *Per capita* origination and extinction rates (per lineage Myr) of bivalve families containing and lacking endolithic species. (*c*) Geographical distribution of endolithic species richness today on the continental shelf (depths < 200 m).

hypothesized to relate to mechanical boring [16]. Longer hingelines are expected to constrain the shells' ability to pivot with respect to one another, which may limit boring: a long hingeline constrains the valve movement to be more like that of a book, where the stiff spine attached to the pages all along its length only permits rotation around that attachment plane. However, both short and long hinge-lines (e.g. pholads and petricoline venerids; *Lithophaga* and *Litharca*, respectively) can occur in similar regions of the endolith shell morphospace (figure 3), suggesting that convergence in shell form can accompany biomechanical compensation for ancestral hinge morphology.

Shell sculpture (patterns of relief or topography on the exterior of the shell, distinct from the fine lines sometimes created by the pattern of growth) is known to have a strong functional role in burrowing bivalves [17,59,60], and could also aid endoliths in abrading their substratum. However, sculptural type, extent and magnitude varies greatly among endolithic bivalves. Of the strongly elongate endoliths, some have finely commarginal (concentric) sculpture (figure 3*t*), sometimes with a minor oblique or radial element, but others are smooth (figure 3*o*), or have a characteristic transverse sculpture (e.g. *Lithophaga nigra*, described as a mechanical boring sculpture by Fang & Shen [27]; but see [18] for a rebuttal). *Litharca* (figure 3*j*) has fine radial sculpture, and *Pholas* and *Petricolaria* (figure 3*v*), have cancellate sculpture with a strong radial element. Many pholads (e.g. figure 3*p*,*q*) have separate fields of the shell exterior in which either radials or commarginals dominate, which may focus the boring force against the substratum [61] (cf. [24]), and may trap rock grains during excavation, increasing abrasiveness [11]. Likewise, *Lithophaga* increases its shell's abrasiveness by incorporating tough crystals of fluorapatite [56]. Elsewhere in the morphospace are plicate and sometimes fluted sculptures (e.g. *Tridacna* figure 3*k*) as well as smooth forms (e.g. *Pedum*, figure 3*g*; some gastrochaenids). All of these sculptural types also occur in non-endoliths, suggesting that this morphological axis is unlikely to reveal hidden similarity among endolithic taxa on its own. We cannot yet test whether some interaction of general shell shape and thickness, hinge morphology and sculpture might reveal unique areas of morphospace for endolithic taxa.

(ii) Determinants of disparate shell morphology among endoliths

Polyphyly contributes to the broad disparity in endolith shell shape, as rock boring is 'unexpectedly widespread' across Metazoa [62]. Within Bivalvia, it occurs in multiple distantly related families, and has arisen several times within the Mytilidae alone [55,63]. Endoliths tend to resemble the shell morphologies of the non-endolithic members of their respective families more than the morphologies of endoliths from other families, indicating multiple pathways to the endolithic habit and contrasting with the tighter mapping of form to function in shallow and deep soft-sediment burrowers, which are also polyphyletic (figure 2) [24]. The oldest bivalve endolith (†*Corallidomus*, figure 2*g*; approximately 450 Ma) lies near the periphery of extant endolith morphospace, indicating that subsequent morphological evolution into this function via other, unrelated lineages has tended to drift away from this starting point.

This interpretation considers endoliths as a whole, and the multiple boring methods including chemical and mechanical modes could each have distinctive morphologies and lower disparity. The mean morphologies of chemical and mechanical endoliths do significantly differ, but the distance between those means is on the order of half to a third of the distances to the means for non-endolithic functions (figure 1*b*), and each mode has similarly high respective disparities (figure 2*c*). Most mechanical and chemical endoliths occupy the same region of morphospace, but the edges of the chemical endolith morphospace are set by a small number of very disparate species (figure 2*b*). Similarity in endolithic shell form among families is not concentrated in either chemical or mechanical modes—even the most similar pair of taxa, the chemically boring mytilids and chemically boring venerids, only has 35% of species falling within the 5% threshold of morphological similarity (figure 3*b*,*c*). It should be noted, however, that the boring mechanisms employed by individual species are not always well understood. We surveyed the available literature to assign taxa to classes (references are listed for each species in electronic supplementary material, dataset S1), but authors (e.g. [17]) note that both mechanisms are frequently combined. The present classification of endoliths into chemical, mechanical and 'combo' will almost certainly change with further research into their biology; however, any such reclassification is unlikely to produce a strongly different pattern than that reported here.

These patterns suggest that biomechanical demands on shell shape are probably reduced for both mechanical and chemical borers, respectively, permitting even *Tridacna* (figure 3*k*) to penetrate hard substrata despite presenting its largest cross-sectional area to the substratum. The hydrodynamics of mechanical boring may also relax selection for ancestral shell forms that were efficient in penetrating soft substrata. Burrowing in soft substrata requires displacement of incompressible water or fluidized sediment, whereas boring may actually relax the requirement to concentrate hydraulic pressure at a given geometric point of the shell to penetrate hard substrata. In fact, fluid pressure in the mantle cavity and haemocoel is reduced in boring versus burrowing [16]. Thus, successful ingress into rocks may not require extensive morphological alteration of the shell from non-endolithic ancestral states.

Even similar shell shapes need not indicate similar boring mechanics. For instance, some elongate pholads have an anterior gape, through which their suctorial foot clamps to the substratum to facilitate their boring action [11], but this feature is absent in many other endolithic species with otherwise similar cylindrical shapes (e.g. *Petricolaria* and *Lithophaga*). We cannot quantitatively assess whether these shell shapes are convergent without fossil-derived ancestral morphologies placed in higher-resolution phylogenies (e.g. following [46]), which are not yet available. However, convergence seems likely given (a) the considerable evolutionary distances among these families, with splits ranging in age from 208.5 to 483 Ma (figure 3; these splits also corroborated by the topology of [64] and the fossil ages of families from electronic supplementary material, dataset S1), and (b) the oldest known fossil members of families containing endoliths lack the cylindrical form of most mechanical borers (e.g. for Pholadidae compared to older relatives in Myida figure 3*r*, for Arcidae figure 3*i*, for Mytilidae figure 3*f*, and for Veneridae figure 3*y*). However, phylogenetic data are insufficient to exclude pre-adaptation of this shell form within subclades.

Overall, convergence by bivalves on the endolithic habit is evidently more like that of the scenario for woodpeckers than dolphins. Endolithy, much like swimming, is a function in which the entire body interacts with a surrounding medium, so that the bivalve form-function relationship should intuitively conform to the dolphin scenario, but overall we find the opposite. Perhaps the difference in the mode of skeleton construction, with bivalves developing a single accretionary exoskeleton [65] and vertebrates discrete condensations that produce an articulating endoskeleton [66], limits the evolutionary divergence of endolithic bivalves from their ancestral forms toward a single, maximally efficient design. Detailed metabolic and biomechanical data would be needed to test whether disparate endoliths occupy genuinely equivalent adaptive peaks. If so, and if the accretionary exoskeleton is indeed a restriction on morphological innovation, then endoliths may be an example of entries into adaptive zones without strong divergence from ancestral morphologies.

If convergence is viewed as evidence of both adaptation (i.e. extrinsic factors) and constraint (i.e. intrinsic biases) [5,67,68], endolithic bivalves present a particularly complex interplay between those two factors. Convergence among elongate forms suggests a key role for adaptation to the endolithic habit, particularly because convergence is not skewed toward closely related taxa, contrary to Ord & Summers's [69] hypothesis that 'repeated evolution' is more likely to occur among close relatives than among distant relatives. However, the same clades producing highly convergent forms also produce highly disparate ones (e.g. Pholadidae, figure 3*s*), and some endoliths remain close to the morphologies of their source clade (figure 3*g*). Much research will be required to determine whether those clades not gravitating to the most frequent endolithic shapes follow their own pathways because of biases imposed by their genetic or developmental systems, or simply because contingent mutations provided an adequate basis for the transition to endolithy.

(b) Evolutionary pathways to endolithy

The ancestral function for Bivalvia is uncertain: Cambrian bivalves are so small that they may have been either shallow sediment burrowers [70] or epifaunal on matground substrata [71]. Regardless of which of these hypotheses is correct, the independent evolutions of endolithy across the Class raise the complementary pair of questions: how does the endolithic function arise in clades with such varied body plans, and why has the habit *not* arisen elsewhere in the phylogeny? The answers probably involve a mixture of circumstantial and developmental factors (e.g. ecological opportunity and pre-adaptation).

Convergence on the endolithic habit may follow a common sequence of evolutionary change, responding to shared environmental pressures such as escape from predation [23]. The evolution of the chemical pathway may precede and/or facilitate the acquisition of the mechanical one (e.g. in the Mytilidae [18]), easing the predicted strong selection on the shell imparted by mechanical boring. If this evolutionary sequence holds in general, then disparate morphologies become less surprising because the initial invasion of this habit would not depend on mechanical ability. The conspicuous absence of striking or unifying morphological novelties in endoliths also becomes less surprising, as opposed to relatively modest novel features such as the debatedly useful transverse sculpture in some species of *Lithophaga*.

A pathway involving chemical boring as the initial evolutionary step would account for the multiple phylogenetic and function derivations of endolithy. For example, endolithic taxa have evolved from burrowers into soft-sediment (*Platyodon* [Myidae and Pholadidae; see [22,72]]), from byssally attached epifauna (Gastrochaenidae, Mytilidae, *Tridacna crocea* [Cardiidae; see [62]]); and from nestlers (e.g. the Petricolinae [Veneridae], *Litharca* [Arcidae; see [73]], and the geologically oldest known endolith †*Corallidomus scobina* [†Modiolopsidae; see [74]]). Endoliths derived from burrowers or nestlers continued to use their more powerful adductor muscles during the boring sequence, and those derived from epifauna repurposed their pedal or byssal retractor muscles for this task [16,75]). Again, in neither case does the shell morphology necessarily diverge from the ancestral body plan to converge on a similar anatomical solution to the same biomechanical problem (see especially *Tridacna* [21]). Instead, the key, unifying aspects of evolution into endolithy may be found in the interrelated traits of ancestral gill structure and feeding mode.

The feeding mechanism may be important because gills help to clear debris during burrowing and during mechanical boring. The autobranch gill structures seen in most bivalves are more efficient in this task than protobranch and septibranch gills—the latter being modified for live prey capture, which itself is also not conducive to an enclosed lifestyle [76]. Protobranchs also use feeding modes—chemosymbiosis or deposit feeding [76]—that must access soft sediment for nutrition, and therefore are unlikely to be viable from within a borehole. Groups with such anatomical and behavioural constraints would require fundamental changes to their feeding modes in order to evolve into the endolithic habit. As gill structure and trophic modes are highly conserved, evolution into endolithy is unlikely for these clades. However, most bivalves are suspension feeders—the likely primitive feeding mode for bivalves dating back to the mid Cambrian, or at latest the Early Ordovician—suggesting that there has been ample opportunity over the past half-billion years for endolithy to evolve through much of the Class, and yet endolithy is a taxon-poor habit.

(c) Is endolithy an evolutionary dead-end?

The endolithic habit seems to have many ecological advantages—an almost fully enclosed and well-protected refuge from waves, currents, and predators—and it can be accessed by many different morphologies. Endoliths show a 'normal' latitudinal gradient, where richness peaks in the tropics and the biogeography of the functional group conforms to the pattern of Bivalvia overall (figure 4*c*) [77], and so should be as rich as any other function centered on the global tropical maximum. However, endoliths represent only approximately 4% of extant marine bivalve species richness, and by this measure, cannot be viewed as an evolutionary success.

Evolution into endolithy may be a dead-end, in that subsequent diversification stalls, or, at the very least, is damped (see discussion of this general pattern in [78]). The mechanism for this is unclear. Endoliths have evolved in families with typical origination and extinction rates for the Class (figure 4*a*,*b*), indicating that neither 'origination pressure' nor opportunities for experimentation afforded by low extinction rates appear to have determined the occurrence of endoliths across the bivalve tree. Further, the relatively ancient endoliths within large families such as Veneridae and Mytilidae have not become a major fraction of their diversity.

The geological ages of endoliths suggest that this selective pressure or ecological opportunity has spanned nearly all of bivalve evolution (red bars in figure 3*a*). Fossils of the early pteriomorph endolith †*Corallidomus scobina* occur in the Late Ordovician (approx. 450 Ma; [74], and fossils of the earliest endolithic mytilids and gastrochaenids date to the Early Jurassic (approx. 190.8 Ma and 201.3 Ma, respectively; see [23,79], which note borings attributable to gastrochaenids back to the Late Triassic). Within the most derived bivalve superorder, Imparidentia, the venerid subfamily Petricolinae dates to the Late Paleocene (59.2 Ma, [80]). Thus, endoliths are neither relict examples of ancient ecological experiments, nor exclusively young and therefore presumably short-lived, disfavoured novelties. In the two most speciose families containing endoliths, the Mytilidae and Veneridae—each with at least 60 million years to diversify within the habit—there is no evidence that the acquisition of endolithy has acted as a major diversification trigger (i.e. a 'key innovation'). Ruling out these macroevolutionary hypotheses leaves habitat limitation as the most likely explanation for the relatively low taxonomic richness of endolithy.

Rocks, corals and other hardgrounds are abundant in ancient and modern seas, but compared to the vast expanse of sands and muds on the ocean floor, the endolithic habitat is spatially quite limited. This geographical restriction may impede the accumulation of taxonomic diversity, owing to species-area effects [81,82], although the necessary data on seafloor types do not exist at the scale and environmental resolution to address this hypothesis quantitatively. Available habitat likely also limits diversity at local scales, with adverse reactions to crowding observed in many endolithic assemblages (e.g. [19]; see also [17], which shows *Claudiconcha* boring through one another). Such crowding should drive evolution along lines of character displacement, but it has yet to produce a high diversity of endolith taxa. Still unexamined are negative interactions with other organisms such as encrusters that might interfere with larval settlement of endoliths or overgrow their open borings once established.

Regardless of the ultimate driver(s), endolithy has never attained the taxonomic richness seen for other bivalve functions. This may not strictly qualify endolithy as an evolutionary dead-end, but at the very least it is a habit with limited diversification potential. Instead, endolithy is an ancient mode of life, with a remarkable persistence throughout its deep evolutionary history given that its low richness raises the susceptibility to random background and mass extinction.

5. Conclusion

Endolithy appears to be a limited but permeable mode of life for bivalves. Both determinism (as reflected by convergence among distantly related taxa) and contingency (as reflected by the endoliths that remain close to the various morphologies of their source clades) underlie the occupation of endolith morphospace. Although endolithy is accessible by multiple paths, and despite the apparent advantages afforded by avoidance of predators and physical stresses such as wave and current action endolithic clades have not achieved high taxonomic diversity. This low diversity is also surprising given that endolithy has evolved in families showing typical origination and extinction rates for the Bivalvia, and its constituents peak in richness in the tropical West Pacific along with most other bivalve clades and functions. The lack of dramatic diversification among endoliths points to an extrinsic factor (i.e. relatively limited habitat availability impeding taxonomic diversification within this distinctive function), although this hypothesis is supported more by elimination of alternatives than by direct tests. Morphological and functional novelties are often seen as key to invading new ecological space (e.g. cichlids, sticklebacks; see also [5,83]), but endolithy is not a functional challenge with a single morphological solution across Bivalvia: contrary to expectations of homoplasy shaped by previous studies in bivalves that burrow, swim or attach epifaunally, endolith shell shape has been affected by both function and family membership. Endolith origin and persistence may be due to the interaction of opportunities (i.e. proximity to suitable habitat both geographically and functionally) and widespread availability of suitable developmental variation on which selection can act, enabling the invasion of this habit along multiple phenotypic lines among multiple clades.

Ethics. All biological materials used in this study were sourced from museum collections. No live animals were used in this study.

Data accessibility. Dataset S1 is available from Dryad [84], containing *Collins_etal_dataset.xlsx* that provides endolithic bivalve species with references, the biogeographic distribution of endolithic species today, the taxonomic identity of specimens sampled for morphological analyses and the links to their mesh data on Morphosource (Project ID 000483849), landmarks used in morphological analysis, and the family level phylogeny used in analyses. Code to reproduce analyses and figures is in *Collins_etal_code. R* in Zenodo [85].

The data are provided in electronic supplementary material [86].

Authors' contributions. K.S.C.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; S.M.E.: data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; D.J.: data curation, formal analysis, funding acquisition, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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