



Subject Areas:

biomechanics, structural biology, biomimetics

Keywords:

leech cocoon, graded cellular architecture, Voronoi tessellation, radial load capacity, functionally graded materials, biomimetic structures

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Design principles of the *Hirudo* cocoon wall: graded Voronoi architecture enhances radial load capacity and stiffness

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The cocoons of *Hirudo* sp. are generally assumed to function primarily as protection against desiccation. However, their wall structure is remarkably complex, comprising a graded cellular architecture that raises the question of whether mechanical protection may be an additional function of the cocoon wall. Here, the three-dimensional cocoon wall structure was characterised by micro-CT imaging, and the measured structural gradients were incorporated into a computational workflow for generating graded Voronoi geometries, to test whether this architecture confers mechanical advantages over a uniform wall of equal mass. Compression testing of 3D-printed model structures implementing this architecture revealed 44 % higher radial load capacity and more than sixfold greater stiffness compared to uniform shell references of equal mass. These results suggest that the graded cellular architecture of the cocoon wall is mechanically consequential, supporting the hypothesis that the cocoon wall serves a mechanical protective function beyond desiccation resistance, and demonstrate the potential of biologically derived graded cellular architectures for load-bearing engineering applications. As the study evaluates abstracted cocoon-inspired model structures rather than native cocoons, direct mechanical testing of biological specimens will be required to establish a complete functional picture.

1. Introduction

The production of a protective cocoon is a defining reproductive trait of Clitellata, a class of Annelida, in which fertilised eggs complete their development enclosed within a hardened proteinaceous wall (see [Figure 1 \(a\)](#)) [1]. This reproductive strategy is particularly consequential in terrestrial and semi-terrestrial species, where embryos are exposed to a range of environmental threats during development [2, 3]. Among clitellates, medicinal leeches (*Hirudo* sp.) are of particular applied interest, as they are commercially bred for FDA-approved hirudotherapy [4]. A better understanding of cocoon structure and function may therefore inform breeding practices and shed light on the ecological role of cocoons in natural habitats. Clitellate cocoons are recognised as multifunctional structures, providing controlled microenvironments for embryonic development while simultaneously protecting against desiccation, predation, and microbial invasion [5]. The functional significance of cocoon wall architecture has been most thoroughly studied in silkworm cocoons (Lepidoptera), which are well-established structural composites. Their graded multilayer wall structures confer high impact resistance and damage tolerance, and it has been argued that mechanical protection of the enclosed pupa is likely

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the primary function of all cocoons [6]. In contrast, the cocoon wall of *Hirudo* sp. has received comparatively little attention. Existing literature has focused primarily on its role in desiccation resistance, with the foam-derived outernetwork hypothesised to trap water via silicon-bearing branch surfaces [7, 8]. Whether the structural complexity of the *Hirudo* sp. cocoon wall serves any mechanical function has not previously been investigated.

As is typical in biology, leeches are subject to multiple selective pressures, including predation, environmental stress, and resource scarcity, placing multifunctional demands on the cocoon. The cocoon of *Hirudo* sp. is deposited directly into soil, where it is exposed to compressive loading from the overlying substrate and from the mechanical activity of soil fauna. The outer wall forms from a foam-derived proteinaceous matrix that solidifies into a three-dimensional network of curved branches [7], a process that inherently generates a stochastic cellular architecture. Whether this architecture is a passive consequence of the secretion process, or whether it has been shaped by selection for mechanical performance, remains an open question.

The cocoon wall of *Hirudo* sp. comprises two structural elements: a closed inner wall and an outer network of thin beams (see Figure 1 (b)). The wall forms from a foamy, viscous liquid that solidifies into the final structure. The physical process by which natural foams develop through the interaction of liquid films surrounding air bubbles is well described by Voronoi tessellation [9], and the outer beam network of the cocoon wall can accordingly be abstracted as a Voronoi lattice.

Radial gradients in the cocoon wall structure have been noted previously [7], but have not been quantified. In a Voronoi lattice, the mechanical properties are governed by beam thickness and cell spacing, both of which may vary continuously across the wall thickness. Graded cellular architectures and Voronoi structures have been employed in mass-optimised applications and shown to produce different and potentially advantageous mechanical behaviour relative to uniform alternatives [10–12]. If the graded Voronoi architecture of the cocoon wall confers greater resistance to external loading, this would support the hypothesis that the cocoon wall serves a mechanical protective function beyond desiccation resistance.

To investigate this, the present study quantifies the cocoon wall as a gradient material, translates the measured architectural parameters into a computational workflow for generating graded Voronoi geometries, and evaluates the mechanical performance of the resulting model structures relative to a uniform shell reference. The workflow employs an implicit modelling approach, which offers substantially higher performance in geometric optimisation tasks [13] and produces structures compatible with additive manufacturing [12]. Because cocoons are small and variable in shape and size, direct mechanical testing using standardised methods is not straightforward. An abstracted structural

model of the cocoon wall was therefore constructed to reproduce the key architectural features observed in the micro-CT data, allowing the mechanical contribution of the architectural gradients to be assessed under controlled conditions and isolating the effect of structural organisation from biological variability.

Based on these considerations, the present study tests whether curved structures with a cocoon-inspired graded Voronoi wall architecture exhibit greater radial load capacity and stiffness than a uniform shell reference of equal mass.

2. Materials and Methods

Cocoon wall architecture was characterised by micro-CT imaging, and the measured structural parameters were used to develop a computational workflow for generating graded Voronoi geometries. The workflow was applied to curved model structures, whose radial load capacity and stiffness were evaluated by compression testing of 3D-printed specimens. An overview of the study workflow is provided in Figure 2.

(a) Sample preparation

Cocoons were provided by a commercial hirudotherapy breeding programme (Animalpharma, Ketzin, Germany). The samples were collected following natural egress of the juvenile leeches and were received pre-dried under ambient conditions, stored in sealed plastic containers. Fresh cocoons were additionally obtained embedded in moist substrate (pH 6.6) prior to hatching, but proved unsuitable for micro-CT analysis: when removed from their controlled environment and exposed to ambient conditions of approximately 50% relative humidity, specimens underwent rapid deformation and substantial changes in mechanical stiffness within approximately 30 min, precluding reliable structural analysis without a controlled humidity scanning environment. All subsequent image analysis was therefore performed on dry cocoon wall sections. *Hirudo* sp. leeches deposit their cocoons by passing them over the head while embedded in moist substrate [8], such that the cocoon is fully enclosed within the soil rather than deposited on its surface.

(b) Micro-CT scans

The three-dimensional structure of the cocoon wall was examined using a micro-CT scanner (Skyscan 1275, Bruker, Billerica, MA, USA). All scans were performed at 40 kV and 60 μ A. One intact cocoon was scanned at a voxel size of 18 μ m. The specimen was mounted upright on a cylindrical polymer support using adhesive wax, which was itself fixed to a circular sample plate by the same method (see Figure 7 (a)).

Ten rectangular wall sections, each dissected from a separate individual cocoon, were prepared for wall section scanning and subsequent image analysis, yielding a total

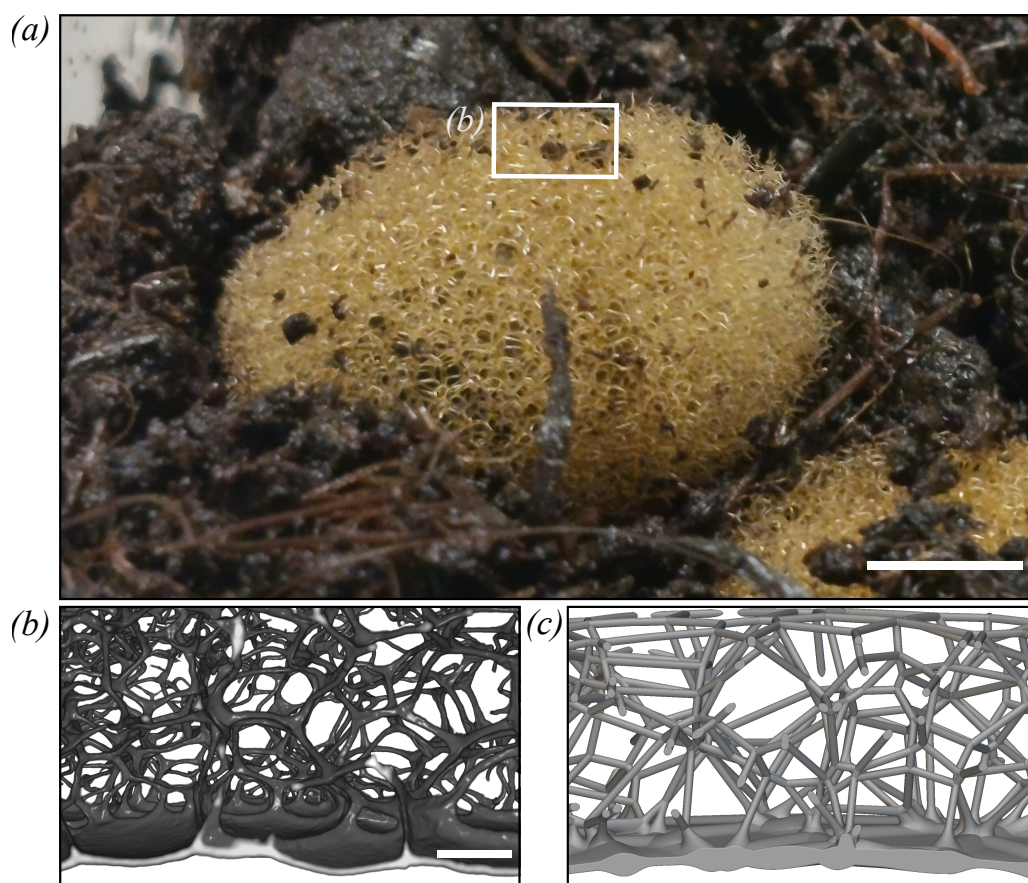


Figure 1: Cocoon of *Hirudo* sp. and its wall structure. (a) A fresh, solidified cocoon embedded in soil (scale bar = 5 mm). (b) Micro-CT cross-section of the cocoon wall (scale bar = 300 μm). (c) Abstracted model structure generated by implicit modelling, comprising a closed inner wall (lower) and an outer Voronoi lattice (upper), reproducing the key architectural features of the cocoon wall.

of ten biological replicates for the gradient measurements reported in Figure 8. The wall sections with side lengths of 4 mm to 6 mm were prepared by scalpel dissection at comparable positions along the flattened lateral faces of the cocoons, where wall curvature is minimal. Specimens were mounted on the tip of a rod-shaped support using adhesive wax and scanned at a voxel size of 7.08 μm . These sections were used for subsequent image analysis.

Raw scan data were reconstructed into image slices using NRecon (v. 2.2.0.6, Bruker, Billerica, MA, USA). Post-alignment was fine-tuned in a single optimisation step using five trials at a parameter increment of 1.0.

(c) Image analysis

Image analysis was performed in Python (v. 3.10, Python Software Foundation) using a Miniconda environment (v. 24.5.0, Anaconda, Inc., Austin, TX, USA) and the Spyder IDE (v. 6.1.0). The packages NumPy, SciPy, and PoreSpy were used to compute pore coordinates and local thicknesses [14–16].

The analysis assumes that the radial axis of the wall section corresponds to one of the Cartesian coordinate

axes. This is justified by the small size of the wall sections relative to the overall cocoon radius, and by rotating each specimen such that the inner wall surface was aligned with a Cartesian plane prior to analysis.

Each scan was first converted to a binary volume by applying a global intensity threshold of 0.3 to the normalised greyscale volume. This threshold was selected by visual inspection of the greyscale intensity histogram of each reconstructed volume, where it fell consistently within the valley between the void and solid material intensity peaks across all ten specimens, correctly separating the two phases without including void-phase noise or excluding solid beam material. No filtering was applied to the images prior to binarisation. The region of interest (ROI) was then defined manually as the largest contiguous area unaffected by specimen preparation, identified by inspecting the scan in multiple orientations and excluding regions with collapsed cells or broken beams. All coordinates were subsequently normalised by the total ROI extent along the radial axis, yielding dimensionless wall-thickness fractions.

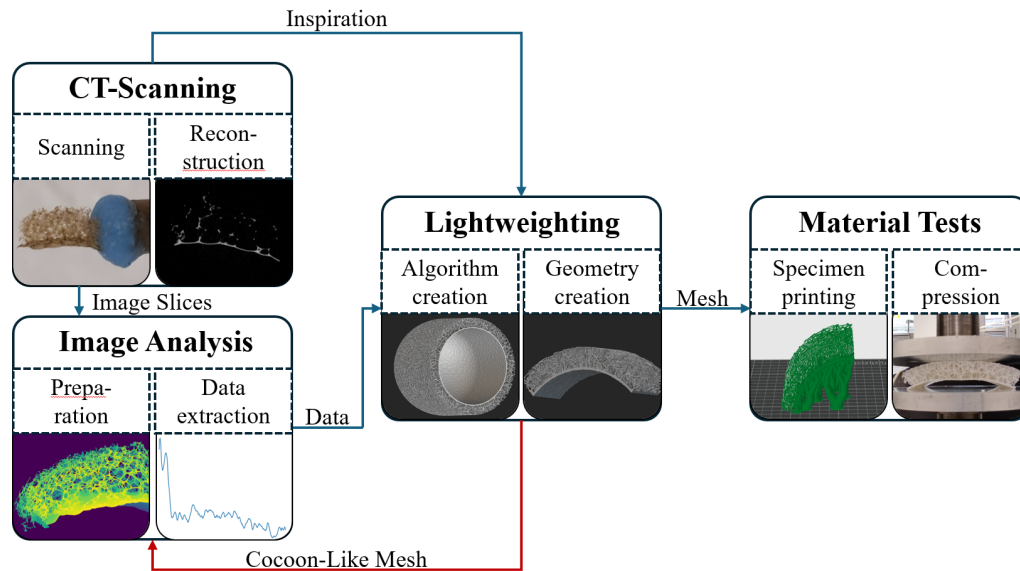


Figure 2: Overview of the workflow used in this study. Blue arrows indicate the transfer of results between successive steps; the red arrow indicates a validation dependency. Representative visualisations of each step are shown below. Within the Lightweighting step, "Algorithm creation" refers to the development of the computational workflow (input variables, gradient lookup tables, and Boolean operations), while "Geometry creation" refers to its application to specific input geometries to produce the model structures used in the study.

Beam thickness was estimated using PoreSpy's local thickness function [16], which operates on the full three-dimensional binary volume. For each voxel belonging to the solid phase, the function computes the diameter of the largest sphere that can be inscribed within the solid phase while overlapping that voxel, and assigns this value as its local thickness. This is a fully three-dimensional metric: the sphere fitting is performed in the complete 3D volume rather than in individual 2D slices, and is therefore independent of beam orientation. This orientation-independence is particularly important for the stochastically organised beam network of the cocoon wall, in which beams are randomly oriented in three dimensions: any residual orientation-related variation in local thickness values would be distributed randomly across all radial positions and could not produce the systematic radial gradient observed in the data.

The resulting local thickness values are proportional to, but not directly equivalent to, physical beam thickness. This proportional measure was considered sufficient for the purpose of this study, which requires only the relative radial gradient in beam thickness — that is, how beam thickness varies across the wall radius — rather than absolute physical beam dimensions. The absolute beam thickness in the computational workflow is set independently via the user-defined *Beam Thickness Scalar* input variable (see Table 1), decoupling the gradient measurement from the absolute scale of the printed geometry. The use of local thickness as a metric for beam and strut thickness in Voronoi-like cellular structures from micro-CT data is well established [17,

18]. The validity of the pipeline as a measure of relative gradient shape was confirmed by applying the image analysis to model geometries with known, manufactured gradient inputs (see Figures S1 and S2). Furthermore, the existence of a radial gradient in beam thickness in the *Hirudo* sp. cocoon wall has been independently documented by Saidel et al. [7] using scanning electron microscopy, confirming that the gradient detected here by local thickness analysis reflects a genuine structural feature of the cocoon wall.

To obtain a one-dimensional radial beam thickness profile, the three-dimensional local thickness map was projected onto the radial axis by averaging the local thickness values of all voxels in the plane perpendicular to the radial axis at each radial position (see Figure 3 (a)). This averaging step reduces the three-dimensional distribution to a single radial profile, which was then fitted with a cubic spline and used as input to the computational workflow.

Cell spacing was analysed by extracting the pore network of each binary volume using the Sub-Network of an Over-segmented Watershed (SNOW) algorithm implemented in PoreSpy (see Figure 3 (b)). Cell (pore) centre coordinates were obtained directly from the network output. For each cell, the distance to its nearest neighbour was calculated using the k-dimensional tree (KD-tree) implementation in SciPy, and this distance was taken as the cell spacing measure. The radial position of each measurement was assigned from the corresponding Cartesian coordinate, consistent with the assumptions described above.

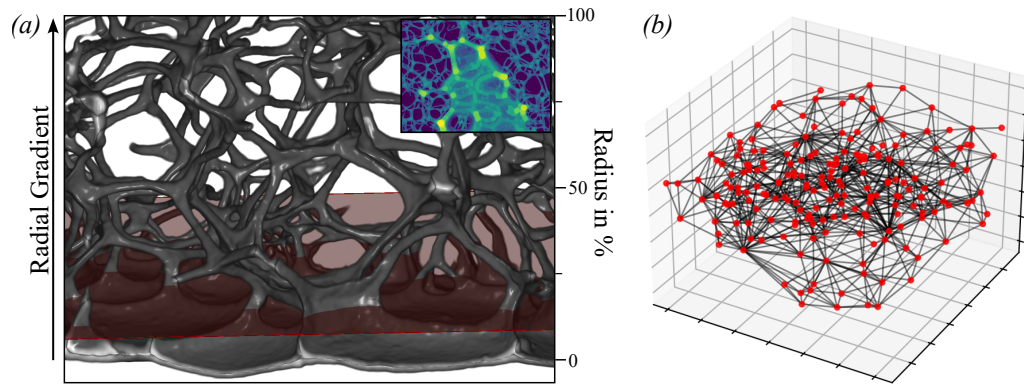


Figure 3: Image analysis procedure. (a) A three-dimensional rendering of a representative wall section volume. Local thickness is computed for every solid-phase voxel in the full 3D volume by fitting the largest inscribed sphere at each voxel location. The cross-sectional plane shown illustrates the subsequent radial averaging step, in which local thickness values of all voxels in a plane perpendicular to the radial axis are averaged into a single radial position value. Repeating this averaging across successive planes along the radial axis yields the one-dimensional beam thickness gradient. A small inset of a wall section scan is color coded with local beam thickness values (warm colours indicate higher local thickness; cool colours indicate lower local thickness). Thicker beams show a higher local thickness and thinner beams a smaller local thickness. (b) SNOW-network of a wall section scan, with cell centres marked as red dots and inter-cell connections as black lines. For each cell, the shortest connection length is taken as the cell spacing measure. Aggregating these values across all cells and noting their radial coordinates yields the cell spacing gradient along the radial axis. Axis tick values are intentionally omitted from this subfigure, as the spatial coordinates of the extracted network are expressed in raw voxel units whose absolute values carry no physical meaning; the radial coordinate is subsequently normalised to dimensionless wall-thickness fractions as described in the Methods.

To enable averaging of beam thickness and cell spacing profiles across specimens with differing radial sampling, each scan was fitted with a continuous curve. Beam thickness profiles were fitted using cubic spline interpolation with continuation extrapolation. Cell spacing data are inherently noisy due to the stochastic nature of Voronoi cell coordinates; these profiles were therefore fitted using the `UnivariateSpline` class in SciPy, which applies a smoothing factor determined by a Generalised Cross-Validation (GCV) algorithm [19], again with continuation extrapolation. The mean and standard deviation of each fitted curve were then evaluated at 100 equally spaced radial positions. The resulting average beam thickness and cell spacing gradients constituted the primary output of the image analysis and served as input to the computational workflow.

(d) Graded Voronoi Geometry Generation

(i) Workflow Logic

The cocoon wall is abstracted into two structural components: a closed inner wall and an outer Voronoi lattice with radial gradients in beam thickness and cell spacing. The interior of the cocoon, inward of the closed wall, is hollow.

Both the closed inner wall and the outer Voronoi lattice are treated as composed of the same material throughout the computational model and physical

specimens. This is consistent with the available literature, which describes both components as derived from the same proteinaceous secretion of the clitellum [7], with the structural distinction between them being morphological rather than compositional. The mechanical distinction between the two components in the model therefore arises entirely from their geometry — the solid inner wall and the porous outer lattice — rather than from material differences. Whether the two components differ in material properties in the native cocoon remains unknown and is identified as a direction for future investigation.

The workflow generates a graded Voronoi geometry from any given input geometry, implementing this abstraction within nTop (v. 5.33.3, nTopology, Inc., New York, NY, USA) using its implicit modelling capabilities. The underlying logic of the workflow is described in Figure 4.

The output geometry reproduces the key architectural features of the cocoon wall while remaining adjustable through four user-defined input variables: *Input Geometry*, *Wall Thickness*, *Beam Thickness Scalar*, and *Cell Spacing Scalar* (see Table 1).

Input Geometry defines the geometry to which the workflow is applied; the outer bounds of the output geometry are identical to it. *Wall Thickness* sets the total thickness of the cocoon-inspired wall, comprising both the closed inner wall and the outer Voronoi lattice; all material inward of this boundary is hollow. *Beam*

Table 1: Input variables of the computational workflow and their effects on the output geometry.

Variable	Type	Effect
<i>Input Geometry</i>	Implicit Body	Determines geometry to apply the workflow to
<i>Wall Thickness</i>	Scalar	Higher values increase mass and stiffness
<i>Beam Thickness Scalar</i>	Scalar	Higher values increase mass and stiffness
<i>Cell Spacing Scalar</i>	Scalar	Lower values increase mass, stiffness, and complexity

275 *Thickness Scalar* and *Cell Spacing Scalar* control the density of the Voronoi lattice by applying a uniform scaling factor to the predetermined gradients. All internal variables are defined relative to *Wall Thickness* or *Input Geometry*, ensuring geometric consistency across different input configurations.

280 The workflow additionally reads *Beam Thickness Data* and *Cell Spacing Data* from external files, converting them into lookup tables that define the radial gradients based on those measured in the cocoon wall. These data represent structural parameters intrinsic to the cocoon architecture and are not intended to be modified under normal use. Following the Boolean union, a morphological smoothing operation with an automatically calculated radius — derived from the *Wall Thickness* and the innermost beam thickness value — is applied at the junction between the inner wall and the outer Voronoi lattice to remove sharp geometric discontinuities at the interface. This produces the locally thickened transition zone visible at the inner wall boundary in Figure 4 (d).

295 Beam thickness and cell spacing were selected as the parameterising features of the outer Voronoi lattice for two complementary reasons. First, these are the only tuneable geometric inputs required to generate a three-dimensional Voronoi lattice in the implicit modelling framework used here, and therefore represent the complete set of variables available within the chosen computational approach. Second, beam thickness and cell spacing are the primary determinants of the relative density of a cellular architecture, which governs its mechanical properties according to established scaling relationships for cellular solids [20]. A radial gradient in these parameters therefore produces a functionally graded cellular material with spatially varying mechanical properties, consistent with the structural logic inferred from the micro-CT data.

(ii) Geometry Generation

310 Three categories of model geometry were produced from thin-walled input geometries, each serving a distinct purpose. A summary is provided in Table 2.

315 Within each category, multiple geometries were produced using different modelling approaches. The cocoon-inspired workflow was applied with varying input parameters, and a uniform shell operation was used to generate reference geometries with a wall thickness adjusted to match the mass of the corresponding cocoon-inspired geometry. Mass reduction is reported as the

percentage reduction in mass of each cocoon-inspired geometry relative to a solid uniform shell of identical outer geometry and *Wall Thickness* (5 mm), computed using the manufacturer-specified density of Bambu Lab PLA Basic of 1240 kg m^{-3} [21]. For all cocoon-inspired geometries, a *Beam Thickness Scalar* of 5, a *Cell Spacing Scalar* of 3, and a *Wall Thickness* of 5 mm were used. These values were selected as the best available compromise between three practical constraints: (i) the beam dimensions of the native cocoon wall are far below the minimum feature size of the FDM printing process (nozzle diameter 0.4 mm), necessitating substantial upscaling; (ii) the scaled geometry required sufficient cell rows across the wall thickness to reproduce the gradient profile meaningfully; and (iii) the overall specimen dimensions were constrained by the compression testing setup. The chosen values produced geometries with approximately 4–5 cell rows across the wall thickness, comparable to that observed in the cocoon wall at the micro-CT voxel size used, while keeping individual beam dimensions above the FDM resolution limit. The scalar values scale the absolute beam dimensions and cell sizes uniformly while preserving the shape of the radial gradient — the relative variation in beam thickness and cell spacing across the wall radius is identical to that measured from the micro-CT data regardless of the scalar values chosen. The resulting model geometries are therefore best understood as scaled, cocoon-inspired architectures rather than direct reproductions of the native cocoon wall, and the mechanical results are interpreted accordingly. A full list of geometries and their input parameters is provided in Table 3.

355 The input geometry for the Suzanne category was prepared in Blender (v.4.1.0, Blender Foundation, Amsterdam, Netherlands) by remeshing the monkey head primitive — a standard benchmark mesh in the computational design and additive manufacturing communities, characterised by complex non-convex surface features including concavities, overhangs, and sharp angular transitions — and then imported into nTop. This geometry was chosen in preference to the cocoon microCT geometry specifically to demonstrate that the workflow is applicable to geometries of arbitrary complexity with no morphological relationship to the biological source, providing stronger evidence of general applicability than a cocoon-shaped input would. Applying the workflow directly to the cocoon microCT geometry is a straightforward extension that is identified as a direction for future work.

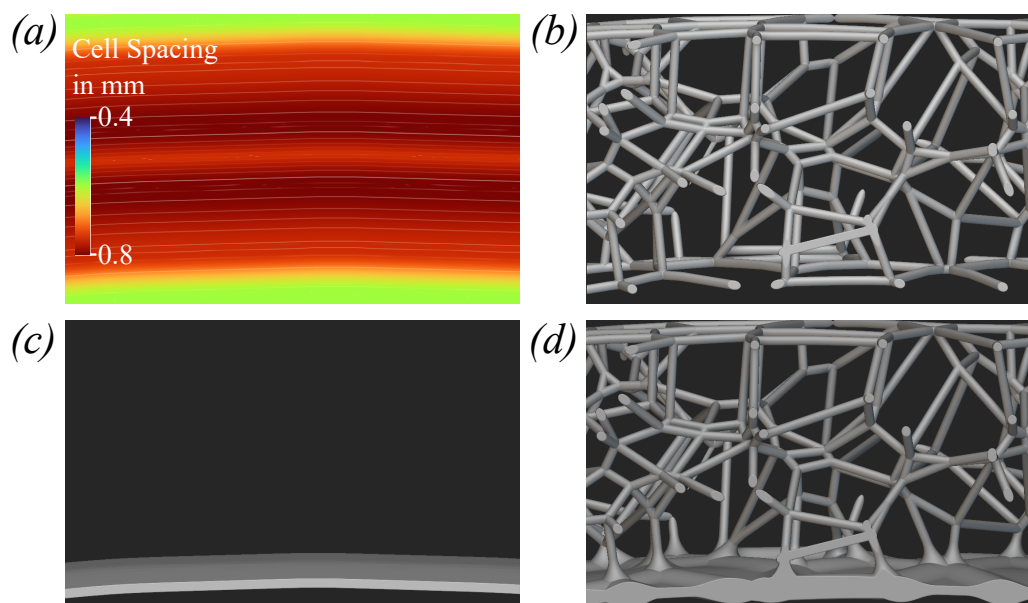


Figure 4: Schematic overview of the key steps in the geometry generation workflow. (a) An input geometry is provided together with the radial gradient data (here: cell spacing gradient) that will parameterise the Voronoi lattice. Colour encodes the local cell spacing value at each cell centre (colour bar: cell spacing as percentage of wall radius; warm colours indicate larger cell spacing, cool colours indicate smaller cell spacing), illustrating the radial gradient in cell spacing incorporated into the computational workflow. (b) A Voronoi lattice is generated within the bounds of the input geometry, incorporating the specified radial gradients. (c) A closed inner wall is added, with thickness equal to the innermost beam thickness value. (d) The two elements are combined into the final cocoon-inspired wall structure via a Boolean union operation. The locally thickened appearance of the inner wall boundary in Figure 4 (d) reflects a morphological smoothing operation applied at the junction between the inner wall and the Voronoi lattice after the Boolean union, rather than a change in nominal wall thickness.

Table 2: Categories of model geometries, their input geometries, and their purpose within the study.

Category	Input Geometry	Purpose
Suzanne	Monkey primitive	Workflow showcase
Curved	Cylinder section	Compression testing
Flat	Cube face	Image analysis validation

Table 3: List of all model geometries and the input parameters used to generate them. Geometries for which no input parameters are listed were produced using a uniform shell operation; all others were generated using the cocoon-inspired workflow.

Geometry	Input Data
Curved Cocoon	Cocoon Average
Curved Shell	None
Suzanne	Cocoon Average
Flat Constant	Manufactured Constant
Flat Linear	Manufactured Linear

An example of the workflow output and its further processing using FEA is shown in Figure 6.

(e) Compression Testing

Two mechanical properties were defined for this investigation. The term “radial load capacity” has been used in the context of radially compressed bearings [22, 23], which are hollow profiles subject to external radial

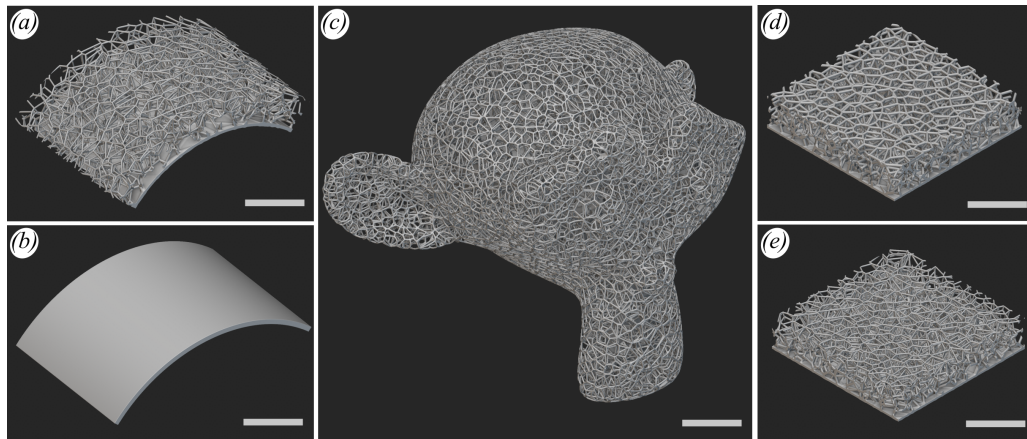


Figure 5: Model geometries used in the study. (a) Curved Cocoon and (b) Curved Shell (scale bar = 20 mm) were used for mechanical testing. (c) Suzanne (scale bar = 10 mm) was used to demonstrate the applicability of the workflow to geometries with complex surface features. (d) Flat Constant and (e) Flat Linear (scale bar = 20 mm) were used for validation of the image analysis.

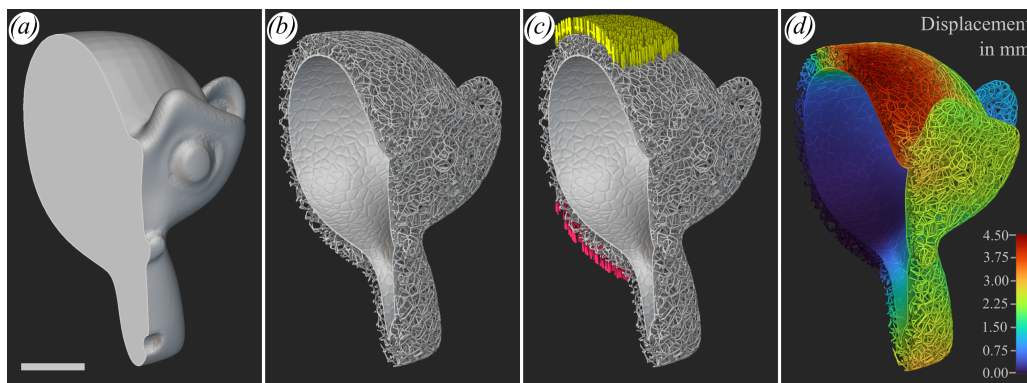


Figure 6: Showcase of the computational workflow applied to a complex geometry. (a) Input geometry with multiple surface features of varying orientation (scale bar = 10 mm). (b) Resulting cocoon-inspired output geometry, in which the workflow has preserved the surface features while hollowing the interior and generating a graded Voronoi wall structure. (c) Exemplary boundary conditions for finite element analysis (FEA), with yellow arrows indicating a compressive load of 0.002 N and red arrows indicating fixed displacement constraints. (d) Exemplary FEA results obtained under these boundary conditions.

loads, but no precise definition has been provided in the literature. By inference from its established use, radial load capacity is here defined as the maximum external compressive force that can be applied radially to a hollow profile without causing failure. Radial stiffness is defined as the slope of the initial linear force-displacement response of a profile under radial compression.

The cross-sectional geometry of a cocoon is a hollow profile. Given the natural orientation of cocoons deposited in soil, external mechanical loads are most likely applied radially. Radial load capacity and stiffness were therefore selected as the relevant mechanical properties for this investigation.

Compression tests were performed on two groups of six 3D-printed model structures each, representing the Curved Cocoon and Curved Shell geometries. As noted

above, these tests characterise cocoon-inspired model structures rather than biological specimens. All twelve specimens were printed using an FDM printer (P1S, Bambu Lab, Shenzhen, China) with a nozzle diameter of 0.4 mm in PLA (PLA Basic, Bambu Lab, Shenzhen, China). The system profile “0.12 mm High Quality BBL X1C” (layer height 0.12 mm) and thermoplastic wire profile “Bambu PLA Basic @BBL X1C” (printing temperature 190 °C to 240 °C) were used with minor adjustments; deviating settings are listed in Table 4. Specimens were oriented with one end flush against the print bed. Prior to testing, all specimens were stored and conditioned at approximately 23 °C and 50 % relative humidity. Specimen masses were measured immediately before compression using a laboratory balance (EMB 200-3, KERN & SOHN GmbH, Balingen, Germany).

Both the Curved Cocoon and Curved Shell geometries were generated from an identical cylindrical section input geometry and share the same outer radius of curvature. The inner radius differs between the two geometries as a direct consequence of the lightweighting process: the graded Voronoi wall of the Curved Cocoon geometry is less dense than the solid wall of the Curved Shell, resulting in a smaller inner radius at equal nominal Wall Thickness. This difference is an intentional feature of the lightweighting approach rather than a confound, as the workflow preserves the outer geometry of any input shape while optimising the internal architecture for mass efficiency.

Compression tests were conducted using a universal testing machine (Z20, ZwickRoell Group, Ulm, Germany) at a crosshead speed of 5 mm min^{-1} . Custom compression platens were machined to accommodate specimens with a square base of $10 \text{ mm} \times 10 \text{ mm}$. Specimens were placed freely between the upper and lower compression platens with no lateral constraint or clamping, resting under gravity with one flat end flush against the lower platen. The specimens remained stable throughout testing without visible lateral movement. Specimens were positioned between the platens in the orientation shown in Figure 5 (a) and (b) and compressed until the force-displacement response became exponential. The initial platen separation was 35 mm and testing was terminated at a separation of 10 mm. All tests were recorded using a smartphone camera (Skyline, HMD, Espoo, Finland) mounted to the testing machine.

(i) Mechanical Property Analysis

Radial load capacity and stiffness were extracted from the force-displacement data of each compression test using a Python script developed in the same environment as the image analysis, with NumPy used for array operations and linear regression [14].

Stiffness was determined individually for each trial. The region of linear response was identified by manual selection, after which the script evaluated all possible linear regressions within that region and selected the fit with the highest coefficient of determination R^2 . Values of R^2 exceeded 0.998 for the cocoon-inspired geometry trials and 0.98 for the uniform shell reference trials.

The force-displacement curves did not exhibit brittle failure, which is typical for compression testing of semi-crystalline polymers. Instead, specimens underwent gradual yielding followed by geometric densification - the point at which the specimen curvature is fully flattened by the compression platen and further displacement compresses the wall material directly, producing a steep exponential rise in the force-displacement response in both geometry types regardless of wall architecture. Load capacity was therefore defined as the point prior to the onset of densification, determined as the intersection of the force-displacement curve with the linear stiffness function offset by 14.25% along the displacement axis.

This offset was determined empirically by systematic visual inspection of all twelve force-displacement curves: the offset value was varied and the resulting intersection point was evaluated against each curve to identify the value at which the intersection consistently coincided with the end of the initial force plateau across all trials of both geometry types, without overshooting into the exponential densification regime. The value of 14.25% is substantially larger than the offsets used in standardised compression tests of fully dense materials (typically 0.2%), reflecting the substantially greater displacement range over which the curved specimens flatten geometrically before the onset of wall compression. The absolute load capacity values are sensitive to the choice of offset; however, the relative comparison between the two geometry types is more robust, as the pronounced plateau of the Curved Cocoon curve is identifiable across a range of offset values, while the Curved Shell curve shows a more gradual transition without a distinct plateau. The reported 44% performance difference therefore represents a conservative estimate that is preserved across reasonable variation in the offset value, as illustrated in Figure 9 (a).

3. Results

(a) Micro-CT Data

Scans of the intact dry cocoon showed no apparent structural defects at the resolution of the scan. The characteristic closed inner wall surrounded by an outer Voronoi lattice was clearly identifiable in cross-section (see Figure 7 (b) and (c)).

Wall section scans revealed an interconnected network of thin beams forming cells of varying shape and size, consistent with a Voronoi architecture. Representative views are shown in Figure 7 (d), (e), and (f).

(b) Image Analysis

The beam thickness profile exhibits two local maxima within the innermost 20% of the wall radius, attributable to a known measurement artefact of the PoreSpy local thickness algorithm at the solid inner wall boundary (see Discussion and Figure S1), after which it transitions into a near-linear region with a shallow negative slope, decreasing from a mean normalised value of approximately 2.0 at 20% radius to approximately 1.0 at the outer surface — a roughly twofold decrease. The cell spacing profile decreases from approximately 15% of the wall radius at the inner surface to approximately 10% at the outer surface, following a shape resembling a negative quadratic function. Both gradients are therefore present across the full measurable wall radius and are of sufficient magnitude to parameterise the computational workflow.

Table 4: 3D-printing settings deviating from the system profile “0.12mm High Quality BBL X1C”, applied uniformly to all specimens.

Setting	Value
Sparse infill	100 %
Sparse infill pattern	Rectilinear
Enable support	Yes
Brim type	Outer and inner brim

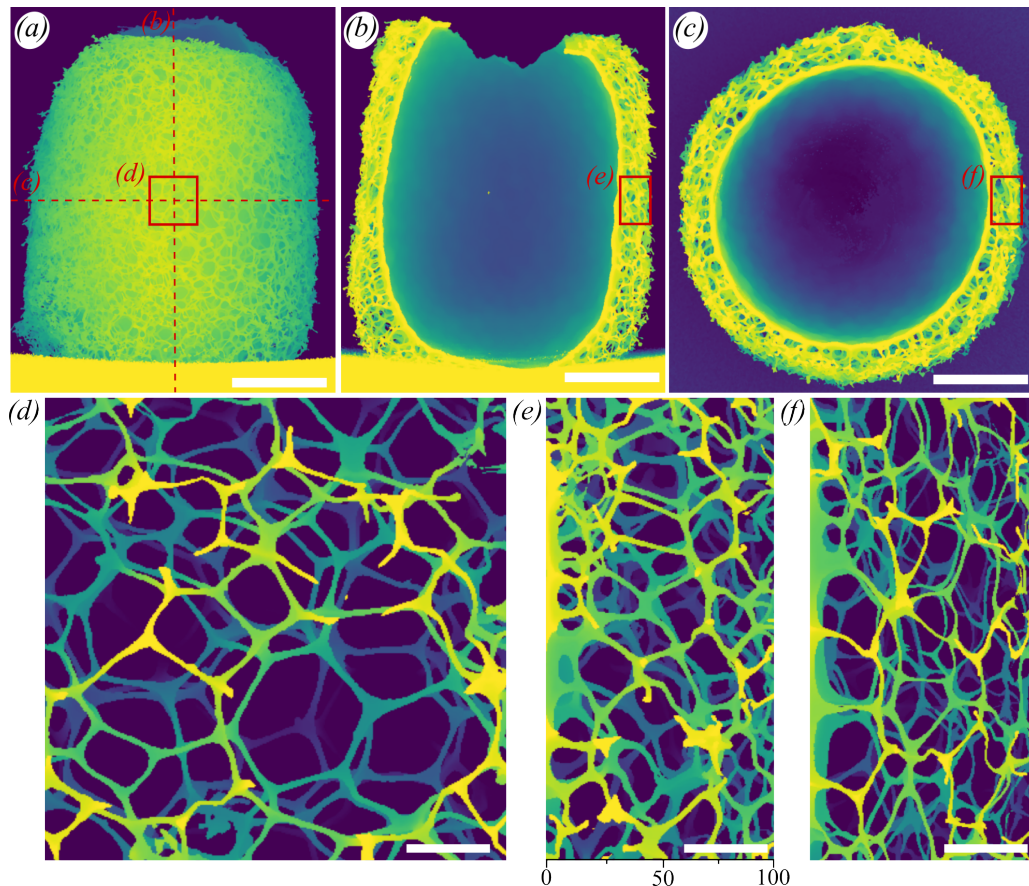


Figure 7: Three-dimensional architecture of the *Hirudo* sp. cocoon wall revealed by micro-CT imaging. (a) The full overview scan of the dry cocoon (scale bar = 3 mm). The cross-sectional planes for (b) and (c) are shown as dashed lines. The approximate region from which wall section specimens were dissected is indicated as a square. (b, c) Cross-sections of the full cocoon scan (scale bar = 3 mm), showing the closed inner wall and outer Voronoi lattice. The rectangular outlines indicate the region of interest used for image analysis as seen from each respective viewing direction; the differing aspect ratios of these outlines in (b) and (c) reflect the three-dimensional shape of the extracted volume viewed from two orthogonal angles rather than an inconsistency in the ROI definition. (d–f) Three orthogonal views of a representative wall section scan (scale bar = 300 μm). Radial coordinates in % are indicated in (d), corresponding to the coordinate system used in the image analysis. The scans reveal an interconnected network of thin beams forming cells of varying shape and size, characteristic of a Voronoi structure. Colour in panels (d–f) encodes viewing depth only (warm colours: closer to the viewer; cool colours: further from the viewer) and carries no quantitative structural information; it is used solely to convey the three-dimensional organisation of the beam network in a 2D image.

(c) Graded Voronoi Geometry Generation

Geometries produced by the cocoon-inspired workflow captured the key architectural features observed in the micro-CT scans, including the closed inner wall

and graded outer Voronoi lattice. The workflow was successfully applied to geometries with complex surface features and allowed further processing by FEA within the same environment, as demonstrated for the Suzanne geometry in Figure 6. The FEA shown for the Suzanne

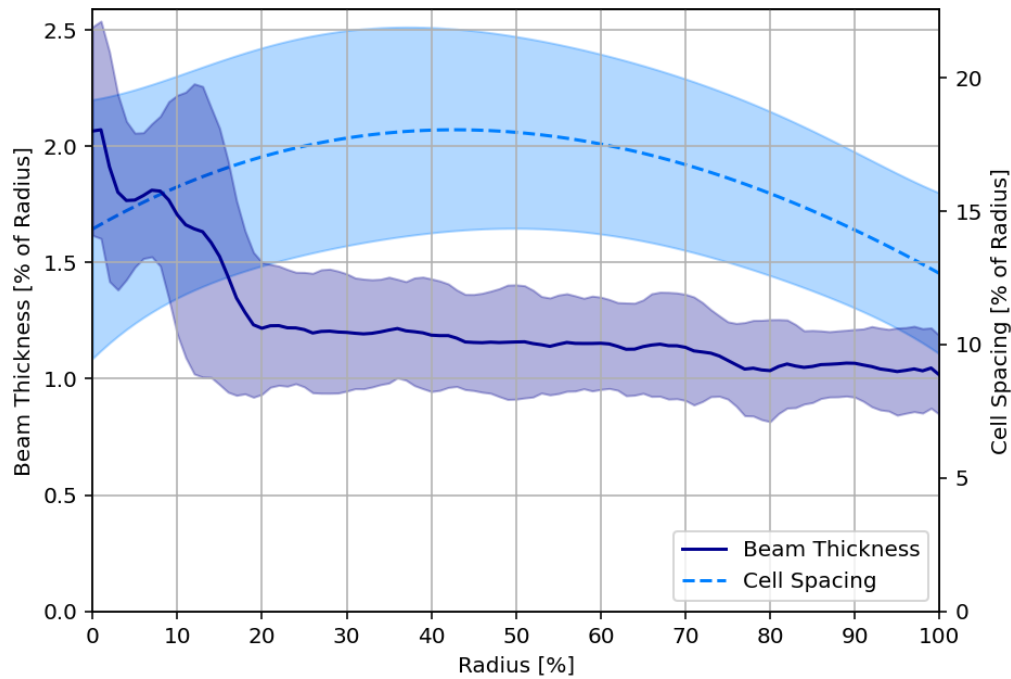


Figure 8: Average beam thickness and cell spacing profiles across the wall radius, derived from ten wall section specimens. Shaded areas represent one standard deviation. The beam thickness profile shows two local maxima in the innermost 20 % of the radius, followed by a near-linear decrease with a shallow gradient. Standard deviation is highest near the inner surface and decreases outward. The cell spacing profile approximates a negative quadratic function, decreasing from a slightly elevated inner value towards the outer surface, with relatively higher standard deviations than those of the beam thickness.

geometry serves specifically to demonstrate the direct compatibility of the workflow output with standard FEA tools within the nTop environment. Finite element analysis was additionally performed on the Curved Cocoon and Curved Shell geometries; however, the absolute force values differed from the experimental measurements by factors of 2.3 and 3.4 respectively, most likely due to an anomalous reaction force distribution arising from the tie constraint used at the implement-specimen interface. These results are therefore not presented quantitatively but are qualitatively consistent with the experimental data in showing substantially higher load resistance for the cocoon-inspired geometry.

Mass reduction is reported as the percentage reduction in mass of each cocoon-inspired geometry relative to a solid uniform shell of identical outer geometry and Wall Thickness (5 mm). With the image-analysis-derived input gradients, the workflow achieved mass reductions of 81.8 % to 83.9 % across the cocoon-inspired geometries. The constant and linear reference input data yielded mass reductions of 70.3 % and 78.0 % respectively. Full results are listed in Table 5.

The validation analysis confirmed that the image analysis pipeline correctly captures real structural gradients in the Voronoi geometry rather than artefacts of the lattice topology, providing confidence that the biological gradients measured from the micro-CT data

represent genuine structural variation in the cocoon wall (see Figure S1, Figure S2).

(d) Compression Testing

The cocoon-inspired Curved Cocoon specimens exhibited a radial load capacity 44 % higher than the Curved Shell reference, and a stiffness more than six times greater (see Table 6). Despite these superior mechanical properties, the Curved Cocoon specimens had a considerably lower mean printed mass of 19.6 ± 0.04 g, compared to 23.7 ± 0.02 g for the Curved Shell specimens, both of which were lower than the predicted digital mass of 27.0 g for both geometries. This discrepancy is attributed to surface material loss during FDM printing, which is proportional to surface area: the Voronoi lattice of the Curved Cocoon geometry presents a substantially higher surface-to-volume ratio than the solid wall of the Curved Shell, resulting in a greater absolute mass deficit relative to the digital model. Since the cocoon-inspired specimens achieved superior mechanical performance at lower printed mass, the mechanical advantage reported here is conservative — a comparison at equal printed mass would be expected to yield an even larger performance difference.

The cocoon-inspired architecture therefore demonstrated superior mechanical performance not only

Table 5: Mass and mass reduction achieved by the computational workflow for each model geometry.

Geometry	Mass in g	Mass Reduction in %
Curved Cocoon	27.0	81.8
Curved Shell	27.0	81.8
Suzanne	13.0	83.2
Flat Constant	31.0	70.3
Flat Linear	22.9	78.0

at equal predicted mass but at substantially lower actual printed mass, confirming that the observed mechanical advantage cannot be attributed to a mass difference favouring the cocoon-inspired specimens and is therefore a conservative estimate of the true performance difference at equal mass.

Force-displacement curves for all trials, together with the average load capacity values and linear stiffness functions, are shown in Figure 9 (a). Curves of the same specimen type were highly reproducible, with near-complete overlap across trials. Both curve types exhibit an initial steep, approximately linear rise, followed by a gradual reduction in slope, and a final exponential increase corresponding to full flattening of the specimen curvature and onset of wall compression. The Curved Cocoon curves show a steeper initial incline and a more pronounced force plateau, while the Curved Shell curves show a shallower incline with a more gradual reduction in slope.

Post-compression specimens are shown in Figure 9 (b)– (e). The Curved Cocoon specimen exhibited permanent deformation of the Voronoi structure with partial recovery of curvature, whereas the Curved Shell specimen recovered its curvature fully. Neither specimen type showed brittle failure.

4. Discussion

The cocoon wall of *Hirudo* sp. has long been regarded primarily as a barrier against desiccation [7, 8]. The present study challenges this view by demonstrating that the graded cellular architecture of the cocoon wall confers substantial mechanical advantages over a uniform wall of equal mass. While the investigation was conducted on abstracted and scaled model structures rather than native cocoons, and therefore cannot directly characterise the mechanical mechanism of the biological structure, the results provide quantitative support for the idea that the structural organisation of the cocoon wall is mechanically consequential, and motivate a broader reassessment of the functional significance of cocoon wall architecture in Clitellata.

The broader biological context supports this reinterpretation. Clitellate cocoons are well established as multifunctional structures, providing microenvironments for embryonic development while simultaneously guarding against desiccation, predation, and microbial

invasion [5]. The cocoon of *Hirudo* sp. is deposited directly into soil, where it is subject to compressive loading from overlying substrate and from the activity of soil fauna. That the outer wall forms from a foam-derived proteinaceous matrix [7] — a process that inherently generates a stochastic cellular architecture — raises the question of whether this architecture has been shaped by selection for mechanical performance, or whether it is a passive consequence of the secretion process. The present results suggest the former is at least plausible.

In this respect, the *Hirudo* cocoon invites comparison with silkworm cocoons, which represent the most extensively studied class of biological cocoon structures. Silkworm cocoons are recognised as mechanically optimised composite shells, with graded multilayer structures that confer high impact resistance and damage tolerance [6]. Studies of *Bombyx mori* and wild silkworm species have shown that tensile properties are anisotropic, with graded layer properties across the cocoon wall thickness [24]. Finite element analysis of silk cocoons has further shown that their ellipsoidal geometry, laminated layer structure, and graded layer properties collectively contribute to impact resistance [6] — a combination of geometric and architectural factors that parallels the dual-component wall architecture observed in *Hirudo* sp. Wild silkworm cocoons, which are exposed to more demanding environmental conditions than domesticated species, exhibit substantially higher toughness [24], consistent with the hypothesis that mechanical performance is under stronger selective pressure in more exposed ecological settings. *Hirudo* sp. cocoons deposited in soil are similarly exposed to a range of mechanical threats, and the present findings suggest that their wall architecture may reflect analogous selective pressures.

The architectural gradients characterised in this study reflect the dry-state geometry of the cocoon wall, as fresh cocoons proved unsuitable for micro-CT analysis due to rapid structural deformation upon exposure to ambient humidity. The mechanical behaviour of the native cocoon wall in its biologically relevant hydrated state is likely to differ from the dry-state structure reported here, and from the PLA model structures used for compression testing. Hydration is known to substantially affect the mechanical properties of proteinaceous biological materials [7], and a full characterisation of the hydrated cocoon wall architecture would require scanning under controlled

Table 6: Measured radial load capacity and stiffness of the 3D-printed specimens, along with printed specimen mass. Printed masses differ from the predicted digital mass of 27.0 g for both geometries due to surface-area-dependent material loss during FDM printing; see main text for details.

Specimen	Mass in g	Load capacity in N	Stiffness in N/m
Curved Cocoon	19.6 ± 0.04	135 ± 2	50900 ± 382
Curved Shell	23.7 ± 0.02	94 ± 7	8324 ± 195

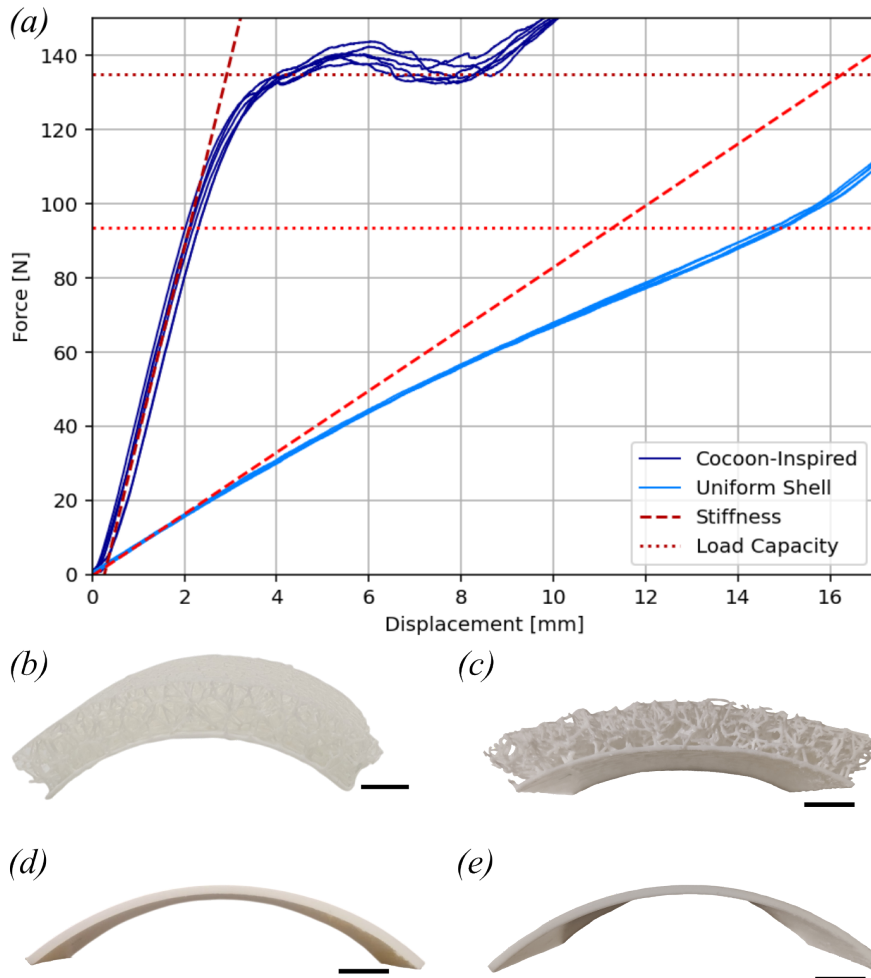


Figure 9: Results of the compression tests. (a) Force-displacement curves for all specimens, with average radial load capacities and linear stiffness functions indicated. Specimens of the same type showed highly consistent behaviour. Both curve types follow the linear stiffness function initially before transitioning to non-linear behaviour, with a decreasing slope followed by an exponential rise corresponding to full flattening of the specimen curvature and onset of wall compression. The Curved Cocoon specimens show a substantially steeper stiffness and higher load capacity than the Curved Shell references. Curved Cocoon specimen before (b) and after (c) compression (scale bar = 10 mm), showed permanent deformation of the Voronoi wall and only partial recovery of curvature. Curved Shell specimen before (d) and after (e) compression (scale bar = 10 mm) showed full recovery of curvature and no permanent deformation.

humidity conditions. The rapid and dramatic response of fresh cocoons to reduced ambient humidity furthermore suggests that the cocoon wall may actively regulate moisture exchange with the surrounding substrate, a property that warrants further investigation in its own right. Whether the architectural gradients of the

cocoon wall vary with developmental stage is currently unknown. The wall is secreted as a foam that solidifies rapidly after deposition [7], suggesting that the primary gradient architecture is established during secretion; however, progressive changes in material properties during embryonic development cannot be excluded.

Characterising the cocoon wall at multiple developmental stages would be a valuable direction for future work.

The radial gradients in beam thickness and cell spacing were successfully quantified through image analysis of micro-CT scans, advancing the characterisation of the cocoon wall as a functionally graded material. The beam thickness profile within the innermost 20% of the wall radius shows two local maxima that are attributable to a measurement artefact of the PoreSpy local thickness algorithm rather than a biological feature. PoreSpy's local thickness function assigns values by fitting the largest inscribed sphere within the solid phase at each voxel; at the solid inner wall, the inscribed sphere encounters less bounding surface than at individual thin beams, returning artificially elevated values. This interpretation is confirmed by the validation analysis (see Figure S1), in which the same elevated inner region artefact appears when the pipeline is applied to a geometry with a known constant beam thickness. Beam thickness measurements from 20% radius outward are therefore considered reliable. Across this region, and across the full radius for cell spacing, the measured gradients were sufficiently large and consistent to parameterise the computational workflow (see Figure S1 and Figure S2). The observed gradient profile — with higher beam thickness and cell density near the inner wall, decreasing progressively outward — is consistent with an architecture that transitions from a stiff inner boundary layer to a more compliant, energy-absorbing outer network. This structural logic is reminiscent of functionally graded cellular materials used in engineering, where density gradients have been shown to enhance energy absorption under dynamic loading [25].

Compression tests on 3D-printed cocoon-inspired model structures demonstrated 44% greater radial load capacity and more than sixfold higher stiffness compared to a uniform shell reference. These results are consistent with the hypothesis that the graded Voronoi wall architecture serves a mechanical protective function in addition to desiccation resistance. It should be noted that the printed masses of the two specimen types were not equal, despite the computational models being of identical mass. This discrepancy is most likely attributable to surface material loss during additive manufacturing, which would disproportionately affect the specimen with greater surface area. Since the cocoon-inspired specimens achieved superior mechanical performance at lower printed mass, a comparison at truly equal mass would be expected to yield an even larger performance difference.

The substantially higher stiffness of the cocoon-inspired specimens warrants particular attention from a biological perspective. The eggs of *Hirudo* sp. occupy a large proportion of the cocoon interior, leaving little void space to accommodate wall deformation before the eggs themselves bear load. A stiff wall architecture would limit this deformation and protect the developing embryos from mechanical insult. This functional logic

is consistent with observations in silkworm cocoons, where the innermost cocoon layer exhibits markedly enhanced mechanical properties compared to the outer layers, which are understood to be important for efficient mechanical protection of the pupa [24].

The outer radius of curvature was identical for both specimen types, as both were generated from the same cylindrical section input geometry. The difference in inner radius — a direct consequence of the lower density of the Voronoi wall relative to the solid shell — is an inherent feature of the lightweighting approach and contributes to the mechanical advantage of the cocoon-inspired architecture by providing a thicker effective wall at equal or lower mass.

The difference in printed mass between specimen types — 19.6 ± 0.04 g for the Curved Cocoon versus 23.7 ± 0.02 g for the Curved Shell, against a predicted digital mass of 27.0 g for both — is consistent with surface-area-dependent material loss during FDM printing. The cocoon-inspired geometry, with its high surface-to-volume ratio Voronoi lattice, loses proportionally more material during printing than the solid-walled reference. This does not affect the validity of the comparison: the cocoon-inspired architecture demonstrated substantially superior mechanical performance at lower printed mass, meaning the reported advantage is if anything an underestimate of the true performance difference at equal mass.

It must be acknowledged that the cocoon wall is a multifunctional structure, and its architecture likely reflects a compromise between multiple selective pressures rather than optimisation for mechanical performance alone. The closed inner wall, which is conserved across Clitellata, is understood to maintain controlled environmental conditions for the developing eggs [1], and may therefore not be mechanically optimal in isolation. A contribution of the inner wall to mechanical protection cannot, however, be excluded. Investigating model structures of equal mass that omit the inner wall could help to isolate the mechanical contribution of the outer Voronoi lattice, and would be a worthwhile direction for future work. The present model additionally assumes that the inner wall and outer Voronoi lattice are composed of the same material, consistent with their shared proteinaceous origin [7]. If material property differences exist between the two components in the native cocoon — for example through differential cross-linking or hydration — the relative mechanical contributions of the inner wall and outer lattice may differ from the model predictions.

The compression testing programme compared the cocoon-inspired graded Voronoi architecture against a uniform solid shell — the most conservative engineering baseline for a hollow curved profile. Curved Voronoi structures with constant beam thickness and cell spacing were not tested, meaning that the relative contributions of the Voronoi lattice topology and the specific gradient profile to the observed mechanical advantage cannot be fully separated from the present experimental data. The workflow developed here is directly capable of generating

such geometries, and their experimental evaluation alongside a systematic variation of gradient parameters would be a valuable extension of this work. This is identified as a priority for future investigation, alongside the question of whether the mechanical advantage of the graded architecture over a non-graded Voronoi reference is preserved across a range of loading conditions and geometric configurations.

Since this study investigated abstracted model structures rather than native cocoons, it cannot provide a definitive account of the functional purpose of the biological structure. The proteinaceous composition of the cocoon wall [7] will further influence its mechanical behaviour in ways that the PLA model structures cannot replicate. Direct mechanical testing of native cocoons — including nanoindentation of the wall material and compression of intact cocoons — combined with systematic variation of individual architectural parameters, would be necessary to establish a more complete functional picture.

From an engineering perspective, the computational workflow produced model structures with substantial

mass reductions whose mechanical performance may compare favourably with established mass-optimised architectures such as honeycombs. The adaptive nature of the workflow allows it to be applied to geometries of arbitrary complexity and integrated with FEA for downstream optimisation. The present results suggest that the gradient parameters exert a strong influence on mechanical performance independently of mass, indicating that parametric optimisation of the gradient inputs — rather than direct transfer from the biological measurements — could yield further performance gains. A computationally optimised cocoon-inspired architecture may therefore represent a promising approach for mass-optimised applications requiring high radial load capacity and stiffness.

The present results highlight the potential of biologically derived graded cellular architectures for load-bearing engineering applications, and underscore the value of quantitative structural analysis as a tool for uncovering the functional significance of complex biological morphologies.

Ethics. This study used dried, commercially sourced cocoons of *Hirudo* sp. obtained from Animalpharma (Ketzin, Germany). The cocoons were obtained as a by-product of commercial hirudotherapy breeding operations and were not produced specifically for this study. No living animals were used at any stage of the research. All applicable national regulations governing the use of biological material in Germany were strictly observed. In accordance with the 3R principles (Replace, Reduce, Refine), the use of living animals was fully replaced by the analysis of post-mortem biological material and abstracted 3D-printed model structures, thereby eliminating any requirement for animal experimentation.

Data Accessibility. All raw data, scripts, and files used to produce the results presented in this work are available from <https://data.goettingen-research-online.de/privateurl.xhtml?token=f7246fe8-6332-42af-8057-1373c0c67cc3>. A permanent DOI will be provided at acceptance.

Authors' Contributions. T.M.: Conceptualisation, Data curation, Formal analysis, Investigation, Methodology, Software, Visualisation, Writing – original draft, Writing – review & editing. J.M.: Conceptualisation, Supervision, Writing – original draft, Writing – review & editing. J.-H.D.: Conceptualisation, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing Interests. The authors declare no competing interests. Animalpharma (Ketzin, Germany) supplied dried cocoons of *Hirudo* sp. free of charge and had no role in the design of the study, data collection or analysis, interpretation of results, or preparation of this manuscript. No financial or personal relationships with Animalpharma or any other organisation influenced the conduct or reporting of this research.

Funding. This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors. Infrastructure support was provided by the Core Facility for Multidisciplinary Structural Analysis at the HSB (DFG project no. 514140860).

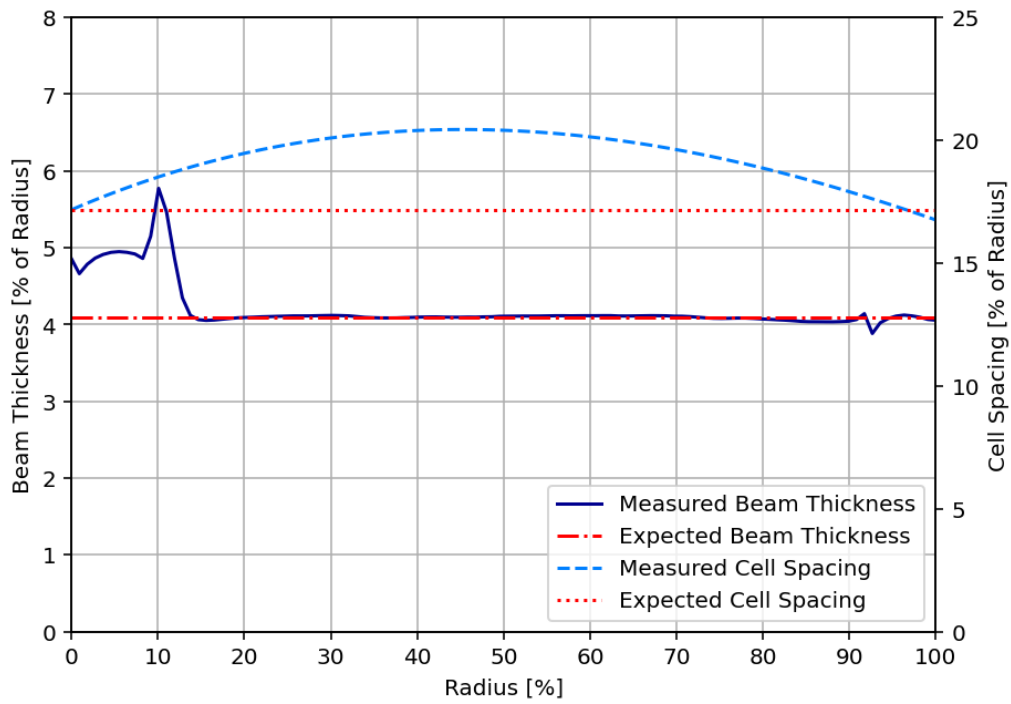
Acknowledgements. The authors thank M. Holzer for assistance with the design and additive manufacturing of the test specimens, and S. Kammer (Animalpharma, Ketzin, Germany) for providing the *Hirudo* sp. cocoons used in this study. The authors also thank C. Müller (University of Greifswald) for introducing the research topic that ultimately formed the basis of this work. A large language model (Claude, Anthropic, San Francisco, CA, USA) was used to assist with language editing. All scientific content, data, analyses, interpretations, and conclusions are entirely the work of the authors. No AI tools were used to generate or analyse research data, produce figures, or contribute to the intellectual content of this work. The authors take full responsibility for the accuracy and integrity of the manuscript.

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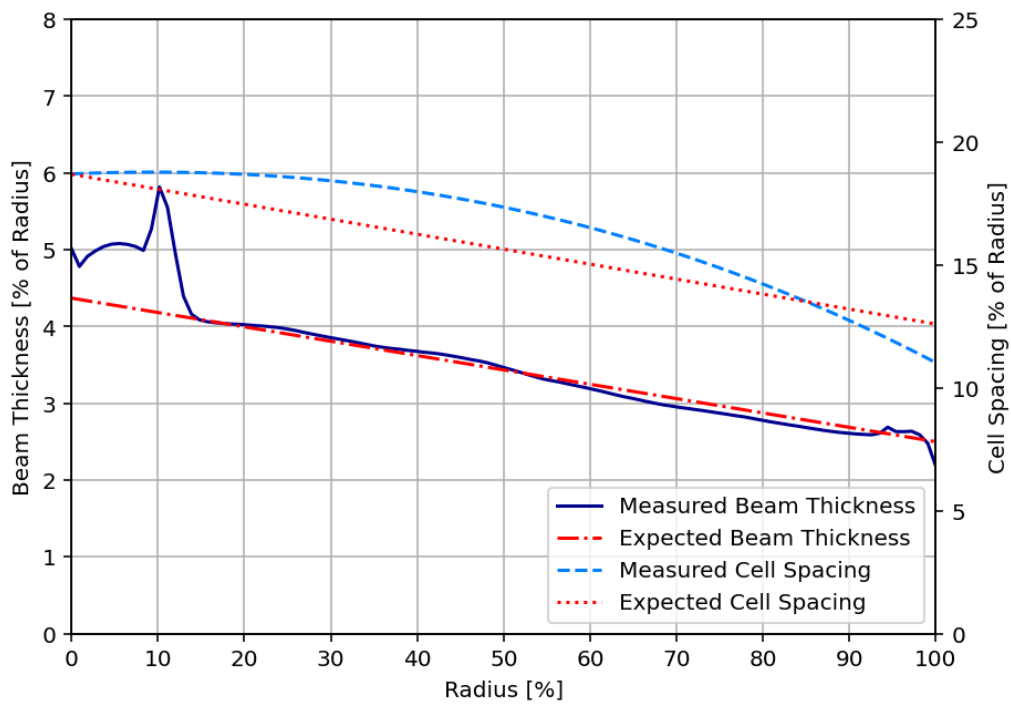
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A. Supplemental Material



(a)



(b)

Figure S1: Validation that the image analysis pipeline measures real structural gradients rather than artefacts of the Voronoi scaffold topology. Two model geometries were generated by the computational workflow using known, manufactured gradient inputs — a perfectly constant gradient (a) and a perfectly linear gradient (b) — and subjected to the full image analysis pipeline. The measured beam thickness and cell spacing profiles are compared against the scaled input data. The general trends of both gradients are correctly reproduced across most of the wall radius, confirming that the pipeline detects genuine structural variation. Deviations are present in cell spacing values near the mid-radius, attributable to boundary effects of the finite lattice, and in beam thickness values below 20% radius, attributable to the measurement artefact at the inner wall boundary described in the main text.

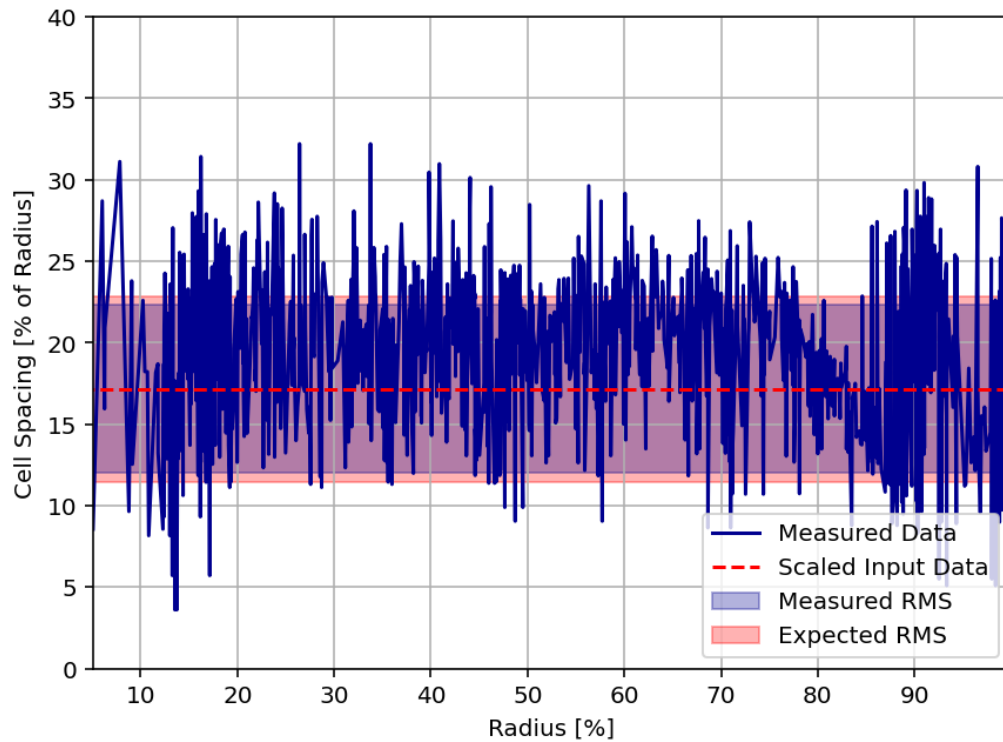


Figure S2: Validation of the stochastic cell spacing noise produced by the computational workflow relative to that measured in biological specimens. Root mean square (RMS) error areas are shown around the constant scaled input data for the Flat Constant geometry. The measured data approximates random white noise around the input curve, and the measured RMS closely reflects the expected RMS calculated from the biological wall section specimens, confirming that the randomisation of cell positions in the computational Voronoi lattice closely reproduces the stochastic variation observed in the native cocoon wall.