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**Quantitative shape analysis of intertesseral joints in tessellated calcified cartilage of sharks and rays (elasmobranchs)**

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The cartilaginous skeleton of sharks and rays (elasmobranchs) comprises an unmineralized hyaline-like cartilage core sheathed in a tessellated layer of calcified cartilage, wrapped in a fibrous perichondrium. The tessellated layer is a composite, composed of minute, mineralized tiles (tesserae), anchored to one another and the surrounding tissue by a collagenous network. This tiled calcified layer allows for skeletal growth, but also provides rigidity to an otherwise flexible skeleton. However, our understanding of the mechanics of the macroscopic tiled composite is limited by the lack of knowledge of the structural interactions between tesserae.

We use high-resolution SR- $\mu$ CT, novel shape-based analysis algorithms and 3D printing to characterize the articulations between tesserae in round stingray *Urolophus halleri*. Although tesserae begin as isolated elements, they grow into contact as animals age: the resultant intertesseral joint is a complex architecture of unmineralized fibrous zones (where fibers connect adjacent tesserae) surrounded by flat regions of close contact, where tesserae are typically  $<2\mu\text{m}$  apart. Tesserae, unlike other natural tilings, neither overlap nor exhibit macroscopic interdigitations; we note, however, that subtle topographic features of contact zone surfaces are mirrored in adjacent tesserae. Coupled with the extreme proximity of neighboring tesserae, this creates an interlocking effect, which we verified with 3d printed tesserae. To further characterize this effect, we developed a triangulated mesh-based shape analysis protocol to evaluate the degree of local and global interlocking of adjacent tesseral edges, identifying variables that define morphological aspects relevant to the mechanics of the tessellated layer, while also offering insight into the structure of tesseral mineralization fronts.

By combining these results with those of ongoing ultrastructural, developmental and material characterization studies of tessellated cartilage, we offer valuable insights into key features of a natural tiled system, distilling design principles for more effective models of bio-inspired, tessellated 3D objects.

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