1. The Hierarchical Structure of Fish Skin

In this study we have investigated the structure and mechanics of a single teleost (ctenoid) fish scale from striped bass *Morone saxatilis*. Like many other structural biological materials,[16–18] the structure of teleost fish scales displays a characteristic hierarchical structure, built over several distinct length scales (Figure 1). At the macroscopic level, the scales are staggered and cover most of the body of the fish (Figure 1a,b). This arrangement provides a continuous barrier to penetration and flexural compliance. When the fish is highly curved (at the end of a swimming stroke), the scales interact more strongly, which stiffens the skin in flexion.[19] The skin then acts as an ''external tendon,'' storing mechanical energy, which can be recovered to facilitate the onset of the next stroke.[15,20] At the mesoscale level, an individual scale from an adult striped bass is a thin plate with an irregular pentagonal shape, about 10 mm in diameter (Figure 1c).

The posterior area of the scale displays rough patterns (ctenii) which offer attractive hydrodynamic properties,[9,10] while the anterior area consists of grooves in the radial direction (radii) and ridges that form circular rings (circuli) around a central area called the ''focus.''[21] Radii and circuli possibly provide increased flexibility and anchoring of the scale, respectively.[10] Teleost scales are composed of collagen fibrils type-I, and are partially mineralized with hydroxyapatite (16–59% mineral content in weight[2,5,22–24]). The outer layer of the scale is significantly more mineralized and often referred to as ''bony layer,'' whereas the inner layer (''basal'' or ''collagen'' layer) is mineralized mostly near the bony layer, but with mineralization pockets proceeding well into the collagen layer.[7,23] In striped bass, bony and collagen layers have approximately the same thickness (100 μm). Using AES

(atomic emission spectroscopy), we measured an average hydroxyapatite mass fraction of 46% for the whole scale. The density of collagen ($1.33 \times 10^3 \, \text{kg} \cdot \text{m}^{-3}$) and hydroxyapatite ($3.17 \times 10^3 \, \text{kg} \cdot \text{m}^{-3}$)[2] were used to estimate the volume fraction of hydroxyapatite as 26%. In another experiment, we separated a scale into two samples by dissecting a few plies off the collagen layer. The upper and lower samples gave hydroxyapatite mass contents of 50% and 14%, respectively (30% and 6% in volume fractions), confirming that the upper region of the scale is significantly more mineralized than the lower region. These results are consistent with reports of a general 20–35% percentage points difference in mineralization between the bony and collagen layers.[25] Bony and collagen layers are cross-ply layered composites, each ply being made of parallel collagen fibrils rotated across layers by angles that can vary from species to species.[25–29] In striped bass, we found that the basal layer is formed of 20–25 plies about 4–5 μm thick each (Figure 1d), where the collagen fibrils are rotated by 90 degrees from one ply to the next (Figure 1e). Cross-ply collagen structures are typically found in natural tissues that undergo multiaxial stresses (shell of soft-shelled turtles,[30] human annulus fibrosus[31]). Several authors have discussed the importance of the plywood nature of the collagen layer to whole fish scale mechanical properties,[2,5,8,32–34] in general by providing the scale with strength along multiple directions. At smaller length scales, individual collagen fibrils, about 50–200 nm in diameter, can be observed on a cross-section of the scale (Figure 1f). Interestingly, we found that in striped bass the 90 degree cross-ply is achieved by alternating layers composed of radial fibrils (''R'' layers) with layers made of circumferential fibrils (''C'' layers), both layers being organized around the focus of the scale (Figure 2). This arrangement is consistent with the growth of individual

0.20 mm. Using this technique, samples were cut at 0, 45, and 90° from the longitudinal direction (anteroposterior axis) of the fish.

The samples were then mounted on a miniature loading stage (Ernest F. Fullam Inc., Latham, NY), which was placed under an upright, reflected light microscope (BX-51M, Olympus, Markham, Canada) equipped with a CCD camera

scales, which occurs by deposition of collagen at the periphery of the scale.[35,36]

2. Tensile Testing on Individual Scales

In order to assess the mechanical response of individual scales, we performed tensile tests in hydrated conditions on small tensile samples prepared from individual scales. Whole, fresh striped bass (Morone saxatilis) were acquired from a fish supplier (Nature's Catch, Inc., Clarksdale, MS, USA) and kept on ice. Scales were plucked using tweezers and stored in a freezer at −20 °C until tested. Before the test, the scales were removed from the freezer and put in a water bath for about 5 min for thawing, and then cut into small dog-bone-shaped specimens using a multi-tube rotary hole-punch and dissecting scissors. The resulting samples had a gage length of 4 mm, a gage width of 1.5 mm and an average thickness of about
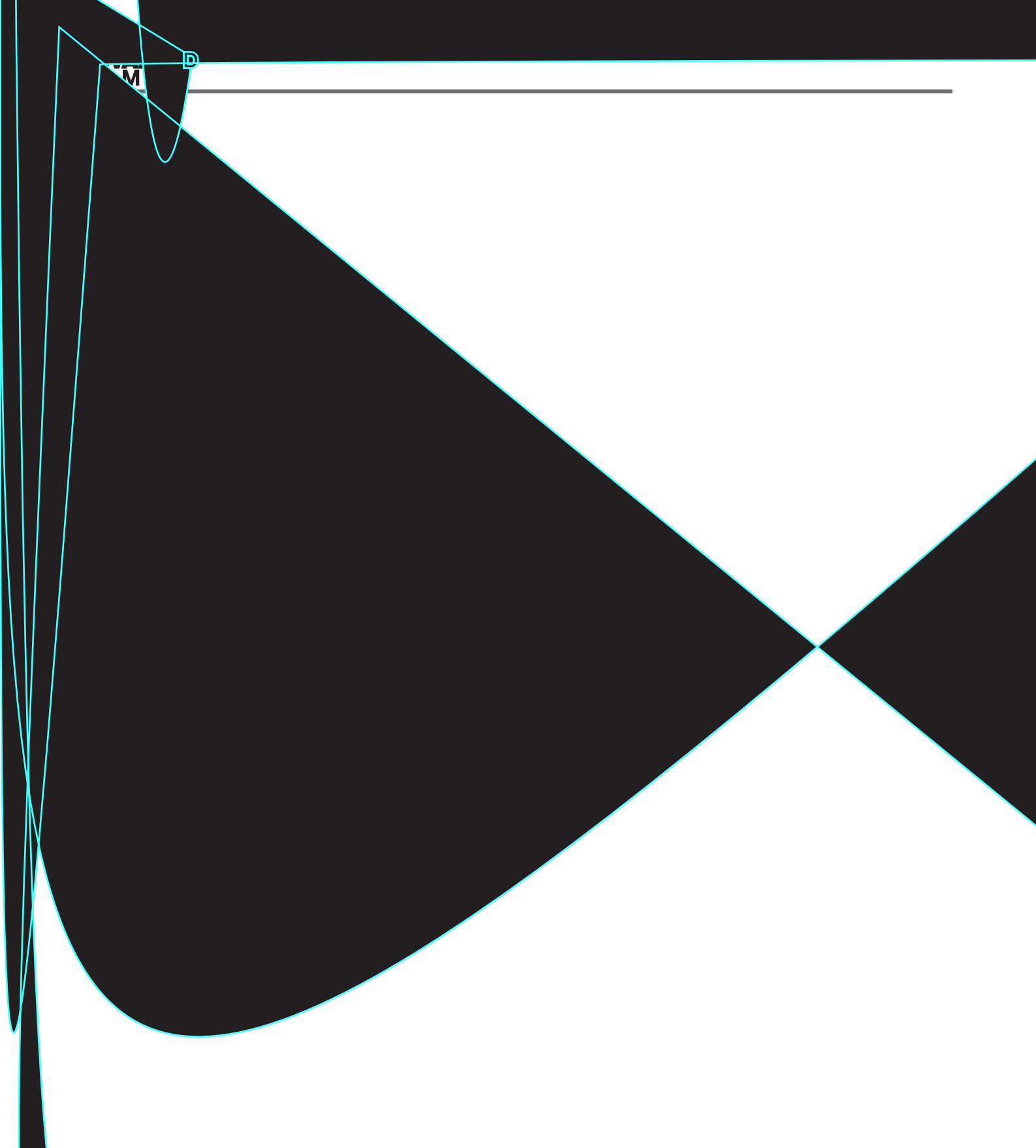
While it was not possible to isolate the bony layer for testing, its properties were inferred from the whole scale and collagen only tensile test results. In the elastic regime, the whole scale behaves like a two-layer, constant strain composite. Since the thickness of the bony and collagen layers is similar, the modulus of the scale is given by:

$$E_S = \frac{1}{2}(E_C + E_B) \tag{1}$$

where E_C and E_B are the Young's moduli of collagen and bony layers, respectively. The modulus of bony layer can then be

area observable with an optical microscope (the scale, while opaque to electrons, is transparent to visible light). The cracking of the bony layer marks the beginning of stage II, dominated by further flexion of the scale, opening of the cross

frictionless hinges. The experiments show circumferential cracks in the region of the hinges, confirming that little or no bending moment can be transmitted though the bony hinge. The second mechanism examined was associated with the collagen, which acts as a retaining membrane for the flaps.

In the model, the collagen layer was assumed to have completely delaminated from the overlying surface of the bony layer, which is consistent with experimental observations towards the end of stage II. The collagen layer then acts

A.2. Deflection of the Flaps

Similarly, point C at the upper tip of the flaps moves to C' upon deflection, and

$$\vec{CC'} = \begin{vmatrix} \dfrac{L}{\sqrt{2}}(\cos\theta-1) + t_B\sin\theta \\ 0 \\ -\dfrac{L}{\sqrt{2}}\sin\theta + t_B(\cos\theta-1) \end{vmatrix} \tag{A.4}$$

The deflection at the loading point is then the z component of $\vec{CC'}$:

$$\delta = \frac{L}{\sqrt{2}}\sin\theta - t_B(\cos\theta-1) \tag{A.5}$$

A.3. Force

Under the concentrated force F/4, the rigid bony flap rotates along the y axis and the loading location changes from C to C'. The force vectors acting on the bony and collagen layers are:

$$\vec{F} = \begin{bmatrix} 0 \\ 0 \\ -F/4 \end{bmatrix} \qquad \vec{T} = \begin{bmatrix} \dfrac{T}{\sqrt{2}} \\ \dfrac{T}{\sqrt{2}} \\ 0 \end{bmatrix} \tag{A.6}$$

As the cross product of the vectors $\vec{OD'}$ and $\vec{T}$ is equivalent to half of the cross product of the vectors $\vec{OC'}$ and $\vec{F}$, then we

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