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# The armored carapace of the boxfish

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ABSTRACT

The boxfish (*Lactoria cornuta*) has a carapace consisting of dermal scutes with a highly mineralized surface plate and a compliant collagen base. This carapace must provide effective protection against predators as it comes at the high cost of reduced mobility and speed. The mineralized hydroxyapatite plates, predominantly hexagonal in shape, are reinforced with raised struts that extend from the center toward the edges of each scute. Below the mineralized plates are non-mineralized collagen fibers arranged in through-the-thickness layers of ladder-like formations. At the interfaces between scutes, the mineralized plates form suture-like teeth structures below which the collagen fibers bridge the gap between neighboring scutes. These sutures are unlike most others as they have no bridging Sharpey's fibers and appear to add little mechanical strength to the overall carapace. It is proposed that the sutured interface either allows for accommodation of the changing pressures of the boxfish's ocean habitat or growth, which occurs without molting or shedding. In both tension and punch testing the mineralized sutures remain relatively intact while most failures occur within the collagen fibers, allowing for the individual scutes to maintain their integrity. This complex structure allows for elevated strength of the carapace through an increase in the stressed area when attacked by predators in both penetrating and crushing modes.

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## 1. Introduction

Many fish, reptiles (e.g. turtle and alligators) [1–5] and mammals (e.g. pangolin and armadillo [6]) have developed dermal armor for the same purpose of defending against the crushing and piercing attacks of predators. While almost all of these armors have developed with similar structures, they are implemented in different ways. One such example is the variety of connection methods between armor plates. These include the overlapping and articulating nature of fish scales [1–4], the non-mineralized collagen fibers (Sharpey's fibers) of armadillo osteoderms [6], the interlocking joints of the bony plates in seahorse armor [5,7,8], and the sutures of leatherback sea turtle scutes [2,3].

Within fish, the scales of the Senegal bichir [1] and alligator gar [4] are prime examples of ganoid scales, which provide protection through articulated arrays of tough bony plates covered by an enamel-like layer. On the other hand, elasmoid scales, such as those found in the arapaima [9,10], bass [11–13], carp [15], and sea bream [14,16] are more flexible with a greater degree of imbrication (overlap). They are also thinner and more flexible than the ganoid scales. Such scales contribute typically to less than 20% of the weight of fish while retaining mobility. In the arapaima and sea bass [9–12], the hardness decreases through the thickness of the scale toward the inside surface [9]. In addition to the mechanical properties of the fish scale layers, there are specific design qualities that dictate the ability of scales to provide protection while still allowing mobility and minimizing weight. These include the amount of overlap or imbrication, the ratio of the scale length to thickness, and the ratio of the scale length to the overall fish length. Fish scales from modern teleost fish are high-performance materials made of cross-plies of collagen type I fibrils reinforced with hydroxyapatite.

Recent studies on this material have demonstrated its remarkable performance in tension and against sharp puncture. The effect of tooth (or a tooth-like indenter) penetration on the scales was recently investigated by Song et al. [17] (for Senegal bichir (*Polypterus senegalus*)), Meyers et al. [9] (for arapaima (*Arapaimas gigas*)), and Zhu et al. [12,13] (for striped sea bass (*Morone saxatilis*)), who identified specific mechanisms. It was shown by Yang et al. [18] that it is difficult for a crack to advance in arapaima scales. A new fracture test setup where the scale is clamped between two pairs of miniature steel plates was developed by Dastjerdi and Barhtelat [19]. By preventing warping of the scales,

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they ensured controlled crack propagation. The work of fracture varied between 15 and 18 kJ/m$^2$ making teleost fish scales one of the toughest biological materials known.

In contrast to these flexible protective layers, the family of Ostraciidae has a rigid carapace [20,21]. Ostraciidae are members of the Tetraodontiformes order [22] that also includes pufferfish, porcupinefish, triggerfish, trunkfish, and ocean sunfish (e.g. Mola Mola) [23]. While the Tetraodontiformes employ many different defensive mechanisms, Ostraciidae are characterized by their boxy appearance (leading to their common name "boxfish") with a carapace composed of rigid scutes (or plates). The boxy shape and rigid carapace considerably restrict the movement of boxfish. Of note, this structure has led to extensive fluid dynamics studies as the unusual shape of the boxfish body and the placement of its fins create a number of vortices around the body and result in a sophisticated self-correcting swimming motion [24–29]. While a model for underwater locomotion, the boxfish is only capable of relatively slow swimming speeds of just above five body lengths per second [30]. Regardless, Ostraciidae have thrived for over 35 million years with effectively the same dermal armor [22].

As a characteristic example of the Ostraciidae armor, the scutes of the boxfish form a biocomposite composed of two basic constituents: mineral and protein. The mineralized component of the scutes is hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$) and the organic constituent is mainly type I collagen, as found in other fish scales [1,4,14,21,31]. The structure of these scutes has been previously described by Besseau and Bouligand [21] who reported that the boxfish primarily has rigid hexagonal scutes formed through helical stacking (a Bouligand structure) of mineralized collagen supporting a mineralized plate. However, there is a current lack of literature related to the mechanical behavior of these scutes and how they might protect the boxfish from predation. Given the success of the boxfish in its natural environment, further understanding of these critical protective mechanics provides insight into bioinspired and materials research. Thus, the objective of this study is to correlate the structure, toughening mechanisms, and failure mechanics of the dermal armor of the boxfish.

## 2. Materials and methods

### 2.1. Boxfish samples

Four boxfish from two sources were used in this study. Three boxfish (*Lactoria cornuta*, catalog numbers SIO 14-20, SIO 95-125, SIO 95-141) were obtained from the Scripps Institution of Oceanography at the University of California (SIO), San Diego and preserved in a semi-dehydrated state in a 1:1 isopropanol (IPA) and water solution (Fig. 1(a)). These samples measured to be ~50 mm in length including the horns and tails (10–15 mm in length). One boxfish was purchased from Live Aquaria (2253 Air Park Road, WI, 54501, USA). This fish was shipped alive but died within a few days and was subsequently stored by freezing for two weeks (Fig. 1(b)). The external appearance of the fish from the two sources is similar. The fresh fish has a length approximately double that of the SIO preserved fish (~100 mm). The scutes are correspondingly larger for the 'fresh' fish: 8 mm vs. 5 mm (in diameter) for the preserved fish. The individual scutes were counted and categorized by shape (e.g. square, pentagonal, hexagonal, or heptagonal) and relative location on the body (e.g. ventral, dorsal, or anterior surface). The flexibility and coherence of the scales can be assessed as shown in Fig. 1(c), where half a fish was sectioned, while its integrity was retained and the scales can be flexed without apparent damage.

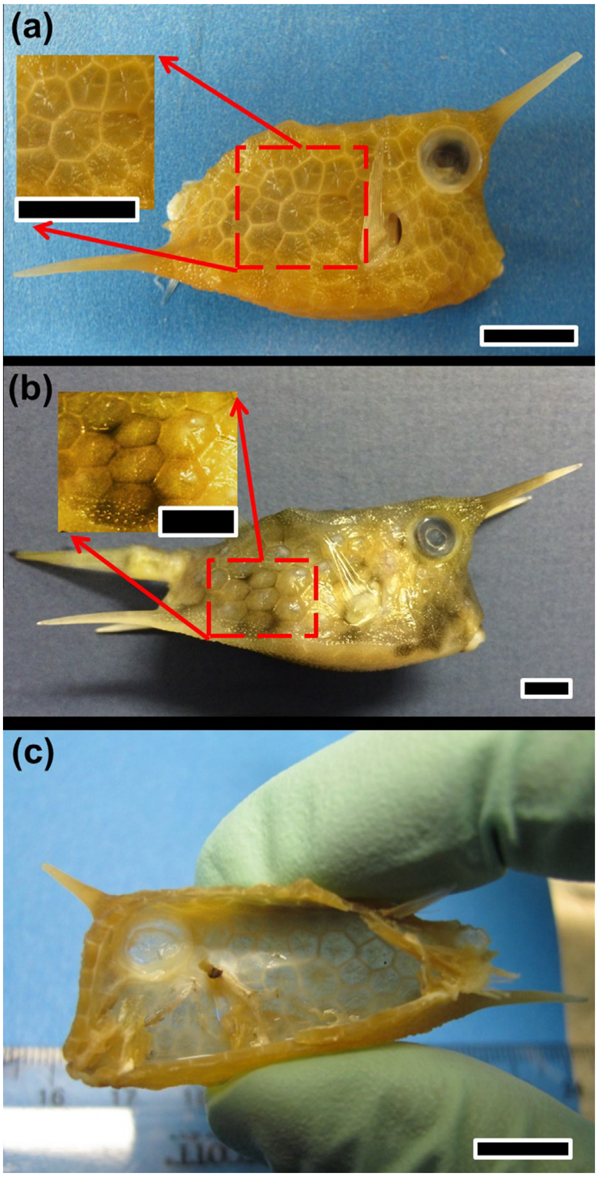

**Fig. 1.** The carapace of the boxfish, *Lactoria cornuta*: (a) Boxfish preserved in 1:1 isopropanol:water showing pentagonal, hexagonal, and heptagonal scutes with sizes between 3–5 mm; (b) Boxfish acquired live; note larger scutes; (c) The flexible and strong carapace under a minor simulated compression load. Scale bars: (a–c) 10 mm.

### 2.2. Structural characterization

The scutes were observed to be composed of a hard plate on top of a compliant base. Each of these components was evaluated to determine the relative quantities of mineral, organic, and water. Full individual scutes, separated collagen tissue (from the base of the scutes, obtained by polishing away the scutes on the surface), and highly mineralized tissue (taken from the horn [32] and assumed to be similar to the mineralized plates on the scutes) were rehydrated in saline solution for ~24 h, and tested by thermogravimetric analysis (TGA) using a SDT Q600 TGA (TA Instruments, New Castle, DE, USA) at a ramp rate of 10 °C/min and a range of 20–800 °C. This procedure has previously been reported for the determination of water, mineral, and protein in biomaterials [33]. In all cases, $N = 5$ samples were tested.

Imaging of the boxfish scutes was performed by optical microscopy (OM) using a VHX-1000 digital microscope system equipped with a CCD camera (Keyence Corporation, Osaka, Japan) and by

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