Flexible Dermal Armor in Nature

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Many animals possess dermal armor, which acts primarily as protection against predators. We illustrate this through examples from both our research and the literature: alligator, fish (alligator gar, arapaima, and Senegal bichir), armadillo, leatherback turtle, and a lizard, the Gila monster. The dermal armor in these animals is flexible and has a hierarchical structure with collagen fibers joining mineralized units (scales, tiles, or plates). This combination significantly increases the strength and flexibility in comparison with a simple monolithic mineral composite or rigid dermal armor. This dermal armor is being studied for future bioinspired armor applications providing increased mobility.

INTRODUCTION

Protection versus predation has been a continuing struggle won by either one or the other, in a competition that has driven evolution. Flexible armor exists in invertebrates (chitons, arthropods), fish, reptiles, and mammals. Thus, this mode of defense has evolved separately in different species by a process of convergent evolution. Dermal armor has been present since the Paleolithic era, ~ 400 million years ago. Placodermi (armored prehistoric fish) fossils with massive armor as ancient as 380 million vears ago have been found. The best-known dermal armor is from the Stegosaurus (150 million years ago), who had osteoderms that bear striking microstructural similarity to those of the crocodile. Another group of armored dinosaurs, Ankylosauria, existed in the Late Cretaceous era (99.6-65.5 million years ago).

Many extant animals possess flexible armor, including mammals (armadillo, pangolin), reptiles [crocodilia, squamata (e.g., Gila monster)], and numerous fish. Figure 1 presents the dermal armor of these representative animals. The shapes of the units (scales or plates) of protection on the armor are varied, but they have common characteristics: low density, high strength, capacity for energy absorption, and flexibility, which depends on the mode in which the scales or plates are joined with each other. The sizes of the units are such that they can conform to the body shape and accommodate its changes, which is a requirement for rapid movement. The flexibility is a definite advantage over the rigid carapaces of, for instance, turtles. Table 1 lists the animals and their different types of scales. Besides protection, it has been reported that some armors have other functionalities, such as the regulation of body temperature,⁶ as in the case of the alligator.

The design strategies used in animals vary considerably. Turtles, armadillos, alligators, and lizards have juxtaposed plates that have different degrees of flexibility and are connected by nonmineralized collagen fibers. In the case of fish, the scales are, for the most, superposed with significant overlap between adjacent scales. Many fish scales have a hard protective external layer and a flexible basal internal layer to maintain intimate contact with the fish body. This also distributes the loads more effectively.

Some questions come to mind. How can the lightweight scales connected by flexible fibers protect these animals? How can they retain their integrity during an attack, even after undergoing damage? What lessons can we derive from the evolutionary developments of natural armor? We provide here some answers to these questions and guidelines toward the design of synthetic flexible armor.



Fig. 1. Some animals having flexible dermal armor: (a) arapaimas,¹ (b) alligator gar,² (c) armadillo,³ (d) alligator,⁴ (e) leatherback turtle, and (f) Gila monster.⁵

PRINCIPLES OF NATURAL FLEXIBLE DERMAL ARMOR

Hierarchical Structure of Selected Animals

One of the main reasons why the small and lightweight scales are strong is their hierarchical structure. Figure 2 shows, in schematic drawings, the hierarchical structures of the dermal armor from selected animals. Arapaima (*Arapaima gigas*), native to South America, is a living fossil and one of the largest freshwater fish in the world; it is shown in Fig. 2a.⁷ The scales are 5–10 cm long and ~4 cm in width with a cross section consisting of an internal layer of collagen (600 μ m thick) and an external layer that is highly mineralized (~1000 μ m thick). The internal layer contains 50- μ m-thick lamellae of oriented collagen fibers that make an angle between 60° and 75° with respect to each other across the thickness,¹³ which can also be observed in the scale of teleost (ray-finned) fish.¹⁴ In Fig. 2, the angle is 90° for simplicity of the drawing. The collagen fibers (1 μ m in diameter) consist of bundles of collagen fibrils (100 nm in diameter). The scales overlap adjacent scales with >60–70% of each scale covered by overlapping scales. Thus, on average, there are three layers of protection: dense lamellae of oriented collagen fibers, dense mineral, and overlapping of scales. These scales have considerable flexibility, as a result of the softer internal collagen layer and can conform to the body as it moves.

	Size of ani	mal				
Animal	Length (m)	Weight (kg)	Size of scales (mm)	Layers	Young's modulus (GPa)	Functionality
Alligator	4	${\sim}360$	31–43	Bone	0.5 (present work)	Protection, regulation
Alligator gar	2.4–3	$\sim\!100$	10 - 40	Ganoine Bone	3.5–5.2* (present work)	Protection (ganoine); buffered
Arapaima	2–2.5	$\sim\!100$	40–100	Bone	$1.2 \pm 0.2 \; (Ref. \; 7)$	Protection (external); flexibility
Bichir	0.05-0.12 (young)	0.1-0.3 (Ref. 9)	2.5–5†	Ganoine Dentin	17 (Ref. 10)	Protection from biting attack ¹¹
Armadillo Leatherback turtle	0.25-0.24 (adult) (Net. 0) 0.5-1 1.8-2.2	$5.4{-}10$ $250{-}700$	${\sim}5$ $30{-}50$	Isopeanne bone Bone Bone	0.43 (Ref. 12) -	Protection ¹²
* Young's modulus wa	s obtained from scales comp	ressed in different	orientations and analyze	d by the Weibull m	ethod; [†] Measured from Ref. 1	0

Another armored fish, the alligator gar (Actractosteus spatula), native to North America can be as long as 3 m and can weigh more than 100 kg. The fish gets its name because of its elongated toothy snout and is covered with scales 10-40 mm in diameter (Fig. 2b). The scales have jagged edges and are attached to the musculature of the fish, and when threatened, the fish flexes the body violently, exposing the cutting edges of the scales and thus creating a surface full of sharp, serrated edges with pointed tips, in an efficient defense mechanism. The scales do not overlap as much as arapaimas scales; only $\sim 30\%$ of the surface of each scale is covered by adjacent scales (Fig. 2b). The scales also consist of two layers: a highly mineralized external layer (ganoine, $\sim 600 \ \mu m$) and an internal layer of bone (~ 3.5 mm). Ganoine, similar to enamel, has >96 wt.% hydroxyapatite (HAP). In contrast to the arapaima scale, the inside contains a complex arrangement of mineralized collagen fibers. Thus, the individual scales are more rigid and are not as flexible as the arapaima scales, which is a prerequisite for slashing and puncturing. Collagen fibers are located between the scales in the overlap part and at the edges of the scales, to connect them together forming rows. The "linejunctions" at the edges of fish scales also connect to adjacent rows of scales. Hence, a fraction of the bony parts of scales are hidden below the other scales in the case of the alligator gar and Senegal birchir.¹⁰

Figure 2c shows the hierarchical structure of the nine-banded armadillo (*Dasypus novemcinctus*) osteoderm.¹² As the name suggests, osteoderms are "bony skin" found in the reptile orders Crocodilia (crocodiles, turtles, caimans) and Testudines (turtles, tortoises, terrapins) and in the mammal order Cingulata (armadillos). The length of armadillo (including the tail) is approximately 0.75 m, and its carapace covers the head, pectoral, banded, pelvic shields, and tail, leaving the soft belly unprotected. The epidermis is α -keratin and serves as a waterproofing layer. Below the epidermis, the osteoderms show three characteristic regions: an internal dense bone, a central porous bone, and an external dense bone layer, as shown in the cross-sectional image in Fig. 2c. This sandwich structure (dense outer sheaths enclosing a porous core) is a configuration found in many animal structures requiring low density along with some energy absorption capability (e.g., skulls and ribs). The osteoderms are hexagonally shaped in the pectoral and pelvic regions and triangular-shaped in the banded shield (torso) region. Nonmineralized collagen fibers (Sharpey's fibers) connect and hold the tiles together. 12,15

Sharpey's fibers are found between bone plates in many animals—for example, the cranium plates are attached by Sharpey's fibers. The Sharpey's fibers, oriented perpendicular to the edges of the tiles, provide flexibility, as shown schematically in



Fig. 3. The collagen fibers also act as a junction between the fish scales. However, the fish scales do not arrange in a juxtaposed style; they are overlapped. The collagen fibers are located between the scales in the overlap part and exist at the edges of the scales to connect them together forming rows. The "line-junction" at the edges of fish scales also connects to another row of fish scales. Hence, a part of the bony parts of scales is hidden below the other scales only leaving the ganoine apparent in the case of the *Polypterus senegalus*¹⁰ and *Actractosteus spatula*.

The leatherback turtle shell has yet a different joining strategy, consisting of intrusions and extrusions in a jagged geometry. These junctions, called sutures, are effective but have less flexibility than the fish scales and armadillo osteoderms. The carapace has seven ridges consisting of the largest plates (Fig. 1e); the regions between the ridges have smaller plates. The plates in the plastron (belly plate) are smaller than those on the carapace. Figure 4a shows two plates on the carapace ridge, whereas Fig. 4b shows an assembly of plates from the plastron. In contrast with the armadillo armor, the shells of the leatherback turtle are irregular and they rely on the sutures between them to connect to each other (Figs. 3, 4). It is obvious that the turtle cannot bend its body as effectively as a fish. Nevertheless, leatherback turtles can dive to great depths (>1000 m) and the flexibility of their carapace enables the contraction of the body associated with the high hydrostatic pressures. The sutures in the leatherback turtle are much less rigid than in other turtle species.



Fig. 3. Three different strategies to provide flexibility: collagen fibers connecting juxtaposed hexagonal osteoderms in armadillo, overlap between bony scales in alligator gar, and suture between osteoderms in leatherback turtle plastron.



Fig. 4. Leatherback turtle plates: (a) two juxtaposed plates from a dorsal ridge and (b) from plastron. Note the irregular-shaped sutures that act as a junction between plates.

Mechanical Design Principles of Natural Armors

The hierarchical microstructure and the unique junctions of the scales discussed earlier can result in outstanding mechanical performance. Figures 5, 6, 7, 8 demonstrate how the structure and junctions can perform outstandingly in mechanical tests. Figure 5a shows alligator gar scales assembled and in cross section. The rhombic-shaped scales are arranged in rows with brown junctions. The ganoine (external layer) is very hard [Vickers hardness number (VHN) ~2.5 GPa] compared with the proximal bone layer (VHN ~0.35 GPa). The nano-

indentation results are higher than the Vickers hardness results but are consistent with other reports for ganoine and bone, 3.6 GPa and 0.7 GPa, respectively.⁷ The ganoine is 5–7 times harder than the bone and compares favorably with enamel in mammal teeth. This is shown by the color coding accompanying the nanoindentation measurements in Fig. 5b, which also shows the reduced modulus. A typical compressive stress–strain curve of the bony part prepared from wet scales loaded in the orientation parallel to the serrated edge is shown in Fig. 5c; there is a clear elastic-pseudo-plastic transition at ~170 MPa; the compression strength of the



Fig. 5. Structural details and mechanical performance of alligator gar scales: (a) scales and cross section; (b) nanoindentation hardness and reduced modulus through the thickness of the scale; (c) compressive stress strain curve for bone portion (d) mineralized collagen fibers; (e) HAP crystals; and (f) ligaments between collagen fibrils.



Fig. 6. Structural details of the arapaima scale (adapted from Ref. 13): (a) scales showing white (proximal) and dark (distal) parts; (b) crosssection showing external triangular mineralized serrations and laminate internal regions; and (c) different layers of collagen fibers with an angle between 60° and 75°.

scale is ~250 MPa, and the Young's modulus is ~6.5 GPa. Compared with the values of cortical bone in mammals, the strength and the Young's modulus are lower, which is the direct result of a larger volume fraction of collagen (shown in Fig. 5d). The specimens can undergo significant deformation prior to failure. During compression, the mineralized collagen fibrils (Fig. 5d, in which the 67 nm spacing of collagen is clearly shown) separate from the HAP crystals (Fig. 5e) and the bonds between collagen fibrils become stretched and then eventually break. Stretched collagen fibrils and the ligaments that attach the collagen fibrils to each other are shown in Fig. 5f in a fractured tensile specimen.

Figure 6a shows the overlapped scales of arapaimas; the dark regions represent the external region exposed to the environment, whereas the light regions are covered by the next row of scales by an overlapping scheme. The cross section of the scale has two layers: the external layer exhibiting triangular ridges (in section) with a spacing of $\sim 200 \ \mu m$ (Fig. 6b), and the internal layer that has a lamellar structure in which the layers are 30-50 μ m thick and comprising collagen fibers. Figure 6c shows the orientation of collagen fibers in adjacent layers with an angle between 60° and 75° . The collagen fibers arranged in different orientations in the lamellae can impede the propagation of cracks. The nanoindentation hardness decreases from the external layer (1.3 GPa) to the internal layer (0.5 GPa).⁷

The scale of Senegal bichir (Polypterus senegalus), extensively studied by Ortiz's group,^{10,16} and shown in Fig. 7, has four layers: ganoine, dentine, isopedine, and bone basal layers. The ganoine layer is composed of rod-like HAP nanocrystals with a length of ~ 220 nm and a width of ~ 40 nm arranged perpendicular to the surface of ganoine. Han et al.¹⁶ investigated the compression behavior and fracture mechanisms of ganoine loaded in three directions with angles of 0° , 45° , and 90° between the rods and the loading direction, as shown in Fig. 7c. The Young's modulus obtained by compression at $\theta = 0^{\circ}$ is the highest (\sim 51.8 GPa), and the one at θ = 45° is the lowest (\sim 36.2 GPa). For the cases of $\theta = 0^{\circ}$ and $\theta = 90^{\circ}$, the cracks propagated almost perpendicular to the surface of the samples in an expected pattern, but when $\theta = 45^{\circ}$, the crack first propagated perpendicular to the sample surface as a result of the contact load direction, and then it changed orientation and propagated along the rods, which make an angle of 45° to the original direction. This mechanism requires shear cracking to form a fracture.

The basic unit of the armadillo osteoderm is the hexagonal tile shown in Fig. 8. In addition to the mineralized collagen fibers inside tile,¹² nonmineralized collagen fibers were observed between tiles (Fig. 8a), providing flexibility. During tension testing, the cracks tend to propagate through the tiles in the dry samples but propagate between the tiles in the wet samples. The mineralized collagen fibers in the wet samples impeded the cracks from



Fig. 7. Structural details and mechanical performance of Senegal bichir fish scale (adapted from Ref. 16): (a) scales; (b) nanopunch test setup on ganoine portion of scale using specimen with a diameter of 1 μ m and a length of 3 μ m; and (c) force–displacement curves of ganoine along different orientations; red lines indicate crack paths between mineral crystals.

traversing the tiles so that the cracks can only choose to travel around the tiles. In tension tests, the collagen fibers between the tiles failed at a stress that is approximately the same as that of the shear test. This result is surprising but easily understandable if one considers that fiber extension is the mechanism of failure for the two cases.

Defense of Fish Scales from Teeth

In the competition for survival, it important to establish whether the protection offered by dermal armor is effective against the local predators. In the case of the arapaima, the piranha is the principal predator. Which one is stronger? The piranha tooth shown in Fig. 9a is sharp, with an angle of ~60°. On the edge of the tooth, small serrations are observed. The hardness of the enamel is ~1.5 GPa, which is higher than that of the mineralized surface of the arapaima scale (~0.55 GPa), suggesting that the piranha may be able to prey on the arapaima. To test this hypothesis, a testing technique was developed by which a piranha tooth was attached to the mechanical testing equipment and loaded on the external region of the overlapped arapaima scales. Several load-penetration curves are shown, showing load drops marking the fracture of the teeth. It is possible that misalignment contributed



Fig. 8. Structural details of armadillo (adapted from Ref. 12): (a) nonmineralized collagen fibers between osteoderms (Sharpey's fibers) and mineral configuration in a deproteinized osteoderm; (b) fracture paths in dry (left) and wet (right) specimens; and (c) shear and tensile loading of osteoderms creating tensile loading of Sharpey's fibers.

to the fracture, but this would also occur in nature. The harder tooth penetrates the softer scale, but as it does this, the area of penetration and friction stresses increase and the process becomes progressively more difficult. The maximum biting force of the piranha was calculated to be below 20 N, and therefore, the loads applied in the test exceeded the piranha biting force significantly, but yet they could not penetrate the scales. Surprisingly, the teeth fractured in most tests; load drops in the force displacement curves mark these fractures. The photographs (Fig. 9b) on the right show the sequence with the tooth gradually penetrating the scale and eventually fracturing. The bottom picture shows the fractured tooth after it was removed from the scales. Thus, the scales are an effective deterrent against piranha attacks. The analysis of scales and the distribution of stresses under them when they are subjected to compression have been carried out by Vernerey and Barthelat.¹⁸ A detailed study by Song et al.¹⁹ used the finite element method and showed the stresses involved in the process for Senegal bichir. In this case, the predator was of the same species.

BIOINSPIRED DESIGN FROM NATURAL ARMOR

It has been shown in this article that scales can protect the host from teeth, whereas the junctions between the scales provide the host with flexibility. The top part of Fig. 10a shows the flexible dermal armor of Senegal bichir. The scales cling to the fish body tightly even when the fish bends in a tortuous shape. Ortiz and collaborators 10,16,19,20 are systematically investigating the shapes of the scales and using this to construct large-scale models where they can establish how the assemblage of scales operates as an armor. This is being applied to the development of synthetic armor. The arapaima scale, consists of a foundation of collagen arranged in successive layers with different orientations of the fibers (shown in Fig. 2a), that supports a highly mineralized external layer. The external layer has ridges which minimize the effects of tensile stresses produced by flexing. A conceptual view of a "flexible" ceramic is shown in Fig. 10a, upon flexing, the tensile stresses are limited to the bottoms of the ridges. This can serve as inspiration for future designs.



Fig. 9. Piranha teeth and their puncturing effect on arapaima scale: (a) red piranha and details of teeth; and (b) force-penetration by piranha tooth through external region of arapaima scale. Note that load drops corresponding to fracture of teeth before full penetration (2 mm) is accomplished. Tooth penetration and fracture shown in right-hand side.¹⁷

"Dragon Skin" (Fig. 10b) is a commercially available armor that was designed from inspiration obtained by the overlap configuration of scales. It consists of overlapped silicon carbide disks that cover the entire surface, which renders the Dragon Skin flexible. A more lightweight, energy-absorbent design would incorporate a porous material in the core, similar to osteoderm construction.

CONCLUSIONS

Animals have created flexible, hard dermal armor through a process of convergent evolution. These dermal armors have developed independently in fish, reptiles, and mammals. Often, the dermal armor of animals possesses a hierarchical structure in which bone tile is the common element, connected by collagen fibers. Different natural armors have different structural units and junctions. They bring flexibility and considerable strength, which can act as a defense against the predators that coexist with them. An important function of this flexible dermal armor is to distribute the load applied locally (by, for instance, teeth) to a larger region, thus decreasing stress concentration and damage to the underlying tissue. This is inspiring researchers to produce a synthetic flexible armor. A synthetic flexible armor is already commercially available and others will hopefully follow.



Fig. 10. Bioinspired flexible dermal armor: (a) conceptual view of flexible ceramic using arapaima scales as bioinspiration;¹⁷ corrugations in ceramic decrease deleterious effects of tensile stresses; and (b) "Dragon Skin" armor.²⁰

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