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almost cylindrical bodies and high-efficiency tails. A glimpse inside would reveal a relatively large brain and a high-performance cardiovascular system, specifically a bigger heart and larger blood volume than in other sharks, to meet the demands of the robust swimming muscles for oxygen and energy, and for removing toxic waste products. The additional oxygen required by these Porsches of the pelagic is supplied by huge gills and large gill slits, and by ram ventilation, keeping the mouth partially open when swimming. And, to add insult to injury (literally!) to the prey, lamnids have striking countershading (dark colored from above, light colored from below) that hinders the ability of prey to detect them.

As if the above adaptations were not enough, the mackerel sharks have evolved a game-changing strategy used by only a handful of other fish, as well as mammals and birds; they elevate their body temperature above that of the environment, known as *endothermy* (the opposite condition, *ectothermy*, refers to the temperature of an organism being the same as that of its environment). The overwhelming majority of bony fish and sharks are ectotherms, since elevating and maintaining a body temperature above that of the heat-sapping water that bathes these animals is a difficult problem to overcome. Members of only seven fish families, including 14 species of tuna, some billfish, five species of mackerel sharks, three species of thresher sharks, and at least two species of manta rays, have evolved ways of trapping heat and elevating their body temperatures above that of the environment.

Why would a marine organism want to raise its body temperature? Temperature is one of the most important environmental factors for all living organisms. For our discussion, let us consider only fish. Temperature affects not only their diversity, abundance, and distribution but also their behavior, activity, growth, development, metabolism, heart rate, digestive rate, and so on. Within the range of temperatures where fish occur, other variables being equal (e.g., prey availability), there are advantages to living at higher temperatures. Within limits, as the environmental temperature increases, there is an increase in the rate of digestion, processing of sensory information, and muscle power.

Consider the effect of temperature on just one factor, metabolic rate, or how fast an organism uses energy. The metabolic rate of most fish, including sharks, as well as amphibians and reptiles, decreases in colder temperatures and increases in warmer ones. Deep-sea sharks, specifically those that do not migrate vertically daily, live in an environment whose temperature is about 39°F (4°C) day and night, across all seasons. These animals have a lower metabolic rate than, say, a Blue Shark at the warmer surface. Sluggish deep-sea sharks thus expend less energy and require less energy from prey than counterparts that inhabit shallow water, which is convenient since there is much less food down deep.

Here then are the advantages of endothermy. First, it enables elevated cruising speeds. All endothermic fish, which include tuna, are fast-swimming, highly mobile predators. In addition, warming the brain increases sensory acuity and processing. Thus, endothermic animals are also better at finding prey and avoiding predators. Endothermy allows mackerel sharks and tuna to move independently of temperature, both latitudinally and vertically within the water column. Cold water, in other words, does not slow them down much. This expands the habitats where they can live.

If being an endotherm is so advantageous, why are only a handful of marine organisms endotherms? First, it is hard to be warm in anything but tropical water. The heat generated by a shark, bony fish, squid, or crab is rapidly lost to the water, about 75,000 times faster than heat is lost in air. Second, trapping body heat requires the evolution of specialized internal systems in the case of fish, or blubber or fur in the case of marine mammals. Although there are big advantages to being an endotherm, ectothermy works well for most marine organisms. Finally, there is a cost to being endothermic: the metabolic furnace that provides the heat, specifically the muscles, requires loads of energy, and thus endothermic marine organisms must be superior predators to supply the calories required to heat the body. And they are!

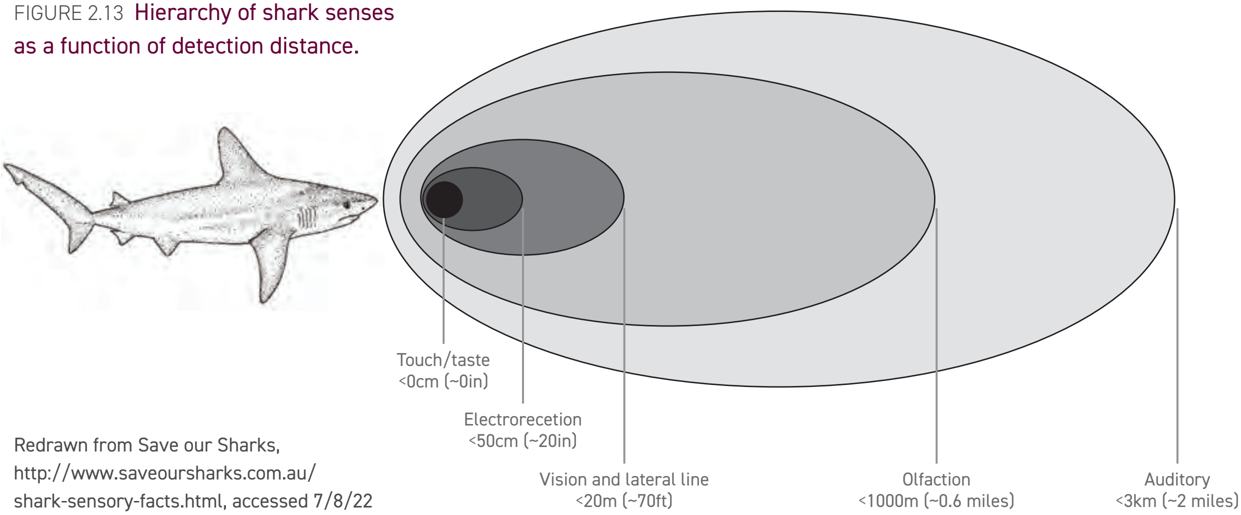
SENSING PREY

Like you, sharks have a suite of senses that allow them to interpret their surroundings and respond. These include those that we humans and other vertebrates possess as well as one or two that are foreign to us. These sensors enable a shark to detect prey, predators, conspecifics (members of the same species), other organisms, and structures. They also allow a shark to orient itself.

A *sense* can be thought of as a group of specialized cells that work as part of a system to detect some form of physical energy or substance in the environment and transmit information about it to the central nervous system, which may then initiate a response. The five traditional human senses are sight, hearing, touch, taste, and smell. These can also be described by the form of energy they detect. Vision is a form of *photoreception*, detecting energy in the form of light waves. Smell and taste represent types of *chemoreception*, responses to chemical stimuli. And touch and hearing represent *mechanoreception*, a means of detecting pressure or distortion. Sharks possess mechanoreceptors, chemoreceptors, and photoreceptors. They also possess *electroreceptors*, capable of detecting an electrical field, and possibly also *magnetoreceptors*, capable of detecting magnetic fields. Although the entire suite of senses integrates to paint a complete sensory picture of the environment, different senses in sharks come into play at various distances and for specific functions (fig. 2.13).

In 2015, a Dutch Caribbean Coast Guard helicopter hovered over a shipwreck survivor in the water near Aruba and was about to rescue him when, according to the *Guardian* newspaper,[6] a shark bit and killed him. Immediately, speculation surfaced that the low-frequency *whomp-whomp-whomp* of the helicopter's rotors played a role in attracting the shark. Is that possible? What sounds attract sharks?

FIGURE 2.13 Hierarchy of shark senses as a function of detection distance.



Redrawn from Save our Sharks, http://www.saveoursharks.com.au/shark-sensory-facts.html, accessed 7/8/22

To answer that question, we must consider mechanoreception, the sense associated with touch, sound, and posture. Water conveys sensory information from mechanical disturbances (sounds and movements) at significantly greater distances than air, so it is no surprise that sharks have adapted to take advantage of this information. Let us consider the ears and lateral line. Yes, sharks have ears, though you would see them only upon dissection, the only external sign being small, paired *endolymphatic pores* (fig. 2.14). These pores open into ducts that lead to the inner ears in the shark's head. Sharks hear in the range of 40–1,500 Hz, with highest sensitivity around 200–400 Hz. The range for humans is reported as 20–20,000 Hz, so sharks hear better in the low-frequency range. Irregular, low-frequency sounds, like those emitted by injured fish, attract sharks. Other sounds, particularly loud ones, repel sharks. Sharks live in an environment that can be relatively noisy. Sounds under a frequency of 1,000 Hz that a shark might encounter and perceive in the marine environment include those associated with swimming fish schools, fish sounds, and waves.

Back to the helicopter and the unfortunate swimmer. While the shark that killed the shipwreck victim could have been attracted to the swimmer using any of its senses, or was simply in the vicinity, the sound of the hovering helicopter unfortunately may have played a role. It certainly did not scare it away, in any case.

The lateral line (fig. 2.15), along with other mechanoreceptors, allows the shark to detect predators, prey, other organisms, and others of its species. It also detects water flow and other physical characteristics of the surroundings and allows for perception of the shark's own body. The lateral lines are canals that run along both sides of the shark from the front of its head to the base of its tail. You can see this line on just about any fish. Along the lateral line, the sensory cells are lined up in a water-filled tube, or canal, under the skin.

Lateral lines are believed to sense *distant touch*, an experience terrestrial organisms lack. You cannot feel a change in air pressure as another human moves close to you, but a shark can feel a pressure change when another shark swims close. And "distant" in this case is an exaggeration, since the lateral line is thought to detect objects only a few body lengths away. If you have ever tried to catch a small fish in a dip net, you know how well this system works. That fish seems to anticipate where your net is coming from. It can do that because it feels the pressure as the net pushes the water ahead of it.

In author Dan's annual Biology of Sharks course at the Bimini Biological Field Station in the Bahamas, one of the students' favorite activities is attracting and hand-feeding juvenile Lemon Sharks[7] in an isolated tidal lagoon. Students spread out along the mangroves, and a *chum bag*, a mesh sack containing minced fish, is positioned on a stake in the sediment where the incoming tide slowly carries pieces of the fish deeper into the lagoon. After perhaps 30 minutes, we begin to see ripples created by the dorsal and caudal fins of the juvenile sharks breaking the water's surface as they wend their way toward us. After conditioning the sharks to take the squid or herring, the students each hand-feed one or two sharks. This exercise is a nice demonstration of how a shark senses its environment. Since the lagoon is less than 330 ft (100 m) long, the sharks likely hear us and initially move away because we are quite noisy. Other senses, including vision, electroreception, and other forms of mechanoreception, cannot come into play at such a distance. What remains is chemoreception, specifically smelling (olfaction) and tasting (gustation).

The ability to detect environmental chemicals like blood is the most ancient of the senses, having evolved over 500 million years ago. Chemoreception in water is quite different than in

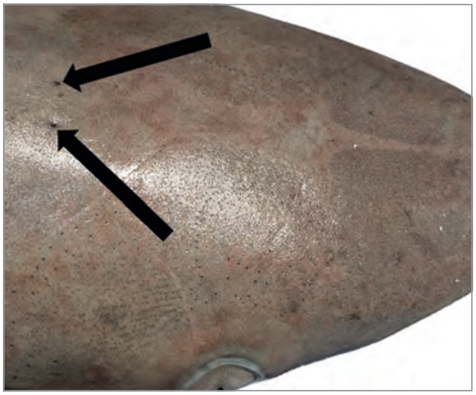
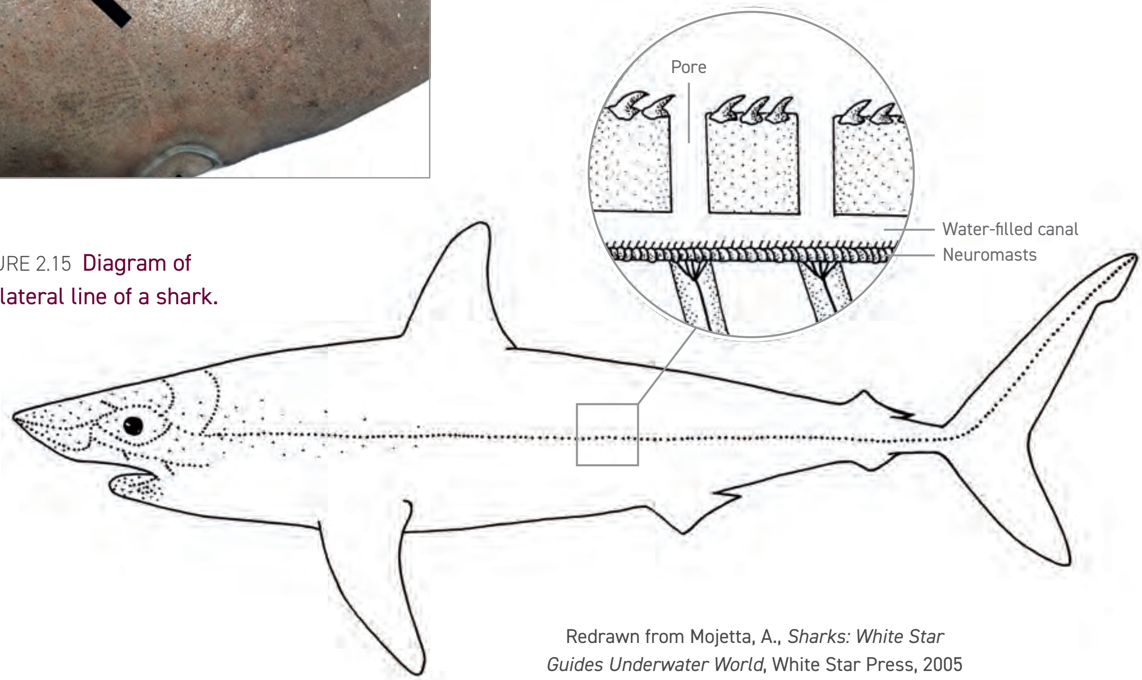


FIGURE 2.14 Endolymphatic pores, external openings of the ears of sharks, on a Blacktip Shark (*Carcharhinus limbatus*).

FIGURE 2.15 Diagram of the lateral line of a shark.



Redrawn from Mojetta, A., *Sharks: White Star Guides Underwater World*, White Star Press, 2005

air since chemicals in water need to be dissolved as opposed to being in the gaseous state in air. Because water is heavier and more resistant to flowing than air, it often moves more slowly, and odors diffuse more slowly as well. Odors also dissipate more quickly in air than in water. Chemoreception is most important for feeding and reproduction.

You may have heard that sharks are "swimming noses" capable of detecting a drop of blood from several miles. This statement is not wrong, but it requires qualification. Yes, sharks have an extremely well-developed sense of smell, but they are not the only bloodhounds of the ocean, since many bony fish have similar sensitivities. For a shark to detect a drop of blood, specific molecules in that blood capable of stimulating the shark's smell receptors must physically encounter these receptors. In other words, the molecules must actually reach the shark's nose, which takes some time.

Back to the lagoon. The chemosensory system of these juvenile Lemon Sharks brings the sharks in. They smell the odorous chum and follow their noses. They then use their other senses in the final stages of locating the food source, which we hope is not our thighs! (And in all the years we have done this, not one shark has made that mistake.)

The organs of smell are paired *olfactory sacs* just above the mouth, in cartilaginous nasal capsules. Water is typically channeled into the nares (you might call these nostrils), the channels that lead into the olfactory sac by flaps on the outermost opening, and then the water moves out through the innermost opening (fig. 2.16). The small distance between the outer and inner opening might mislead you to think that the water that enters travels only a short way before it exits. In reality, the water takes a circuitous path through a heavily folded sensory surface, the *olfactory rosette*, which greatly increases the surface area for sensing environmental chemicals. Think of a spiral playground slide and the extra time it takes to reach the bottom compared to a straight one. The slow transit time ensures that compounds in the water contact the sensors in the rosette. Most sharks must be moving, or there must be a water current, for the system to work.[8] When a shark perceives a chemical stimulus of appropriate strength, it will generally swim toward it while continuously sampling the water, sort of "sniffing" as it goes.

Another form of chemoreception is taste, or gustation. Perhaps surprisingly to you, taste is assumed to have a role secondary to smell and is more specialized in its function. Taste is a way to assess food quality; however, since it is among the most poorly studied senses, its function is not well understood. Taste receptors in sharks are located on taste buds inside the mouth and on the gills. Unlike in mammals, taste receptors are not concentrated on the tongue (yes, sharks have tongues, but theirs are immobile pieces of cartilage, not at all like yours). The location and density of taste receptors vary by species. In bottom-dwelling sharks, these receptors are more evenly distributed throughout the mouth than in open-water species. These different distributions of taste receptors make good sense. Benthic species, such as Nurse Sharks and Brownbanded Bamboo Sharks (*Chiloscyllium punctatum*), often manipulate their prey in their mouths prior to swallowing, during which time they assess the palatability of the ingested item. In pelagic sharks, the highest densities of taste receptors are in areas immediately adjacent to the teeth and at the front of the mouth, the first point of contact when biting a food item. At this critical point, the predator must instantaneously assess whether the item represents food on its menu and is worth

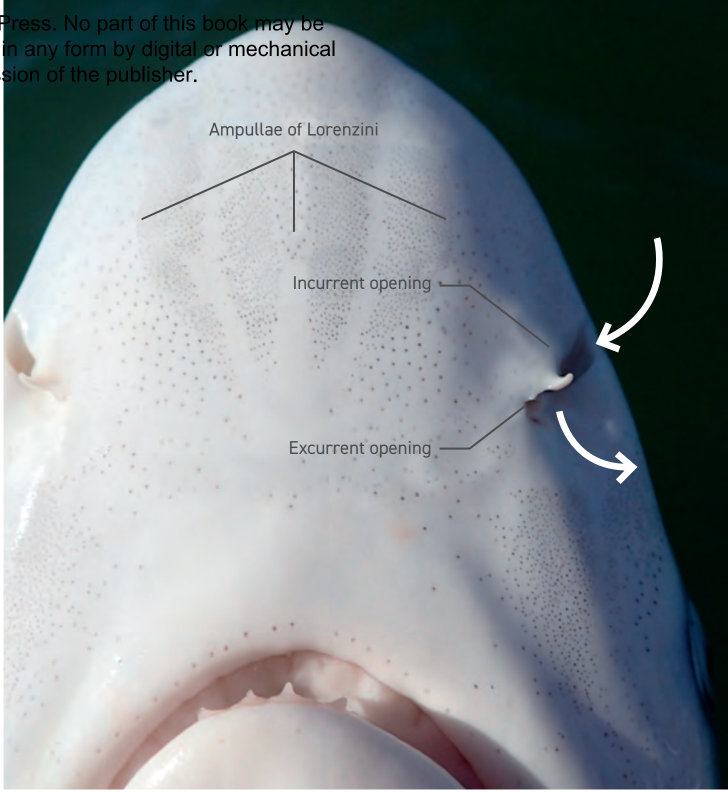


FIGURE 2.16 Incurrent and excurrent openings of the nares (i.e., nostrils) of a shark. White arrows depict direction of water flow. Ampullae of Lorenzini (small pores) are also visible on the underside of the head of this Atlantic Sharpnose Shark (*Rhizoprionodon terraenovae*).

continuing to consume. The concentration of taste receptors near the mouth also explains the *bite-and-release* shark bites we discussed earlier.

The main organ of vision in sharks is, of course, the eye. Sharks have a typical vertebrate, image-forming eye, with some modifications. Sharks possess a *tapetum lucidum*, a tissue behind the retina composed of reflective crystals, which reduces internal glare and scattering of light and improves vision in low-light conditions. This is the same tissue that is responsible for the "deer in the headlights" reflection from the eyes of cats, raccoons, and others. We will see this in other predators, but the tapetum lucidum of a shark is twice as efficient as that of a cat. Light levels can be extremely low underwater.

The lens in sharks is a transparent structure responsible for all the refraction (bending of light) necessary to focus light on the retina. The lens in most species is large and powerful. Unlike the focusing of terrestrial vertebrates, which is achieved by changing the shape of the lens, focusing in sharks is achieved by moving the whole lens backward for far vision or forward for near vision.

The retina is responsible for converting the image that the lens focuses on it into nerve impulses. Like you and most vertebrates, sharks have a duplex retina—that is, the retina houses both rods and cones, the cells responsible for vision in low-light and bright-light conditions, respectively. The presence of cones containing multiple visual pigments implies a basis for color vision, which has been experimentally verified in several shark species.

Another favorite activity of students in our annual Biology of Sharks course in Bimini, Bahamas, is snorkeling with Caribbean Reef Sharks. Typically, within minutes of our arrival at the snorkeling spot sharks appear, having been attracted by the sounds of the boat engine and the water slapping at the hull. They know from experience that this means "snack time." When a piece of bait (not a student!) hits the water, the sharks use their hearing and other mechanosenses to approach the source of the sound. Some detect the odor in the eddies of the water current and move upstream, in the direction of the source. Then, in these clear topical waters, the sharks zero in on the bait using their vision.

This suite of senses often works exquisitely for the first shark at the bait, but sometimes in the dance of the feeding sharks, two sharks will converge on the bait from different locations simultaneously. Both sharks will then trust the more than 400 million years of evolution leading up to that moment, and when they are less than 3 ft (1 m) away from the bait, they will open their mouths almost in unison and deploy their protective nictitating membrane, since their prey in natural circumstances might fight back. This leaves them temporarily blind. If the bait were a live fish, the sharks would detect the minute electrical current that all living organisms emit, and this signal would guide them to the prey with surgical precision, a phenomenon that may also come into play with the dead bait. At this point their systems fool them, because the stronger electrical signal they detect is emanating not from the bait, but from each other. As the bait drifts safely away, at least until the next shark senses it, the two sharks will attempt to bite each other. Fortunately, we have never witnessed any damage done, perhaps because of the gustatory receptors near the teeth that inform each shark of its mistake before the bite is completed.

The electroreceptive system that guides a shark to its destination consists of receptors called ampullae of Lorenzini (fig. 2.16). The ampullae, gel-filled tubes with surface pores, are concentrated on the head of sharks and can detect extremely weak electric fields of other organisms and even inanimate objects. Sharks have been known to sometimes chomp down on boat engines that continually produce a minute electrical current rather than bait for this reason.

TEETH

Sharks have a variety of methods of ingesting food, and these are associated with variation in the form of their teeth. Look at the teeth shown in figure 2.17. Serrated teeth, found in Tiger Sharks, for example, are for shearing. The shark extends its protrusible jaws (see below) into its large prey and swings from side to side, removing a large chunk of the prey, perhaps a dolphin, seal, turtle, or even another shark.

The prey of some sharks are smaller fish that can be swallowed whole, in which case grasping is more important than shearing, and those teeth tend to be long, slender, and nonserrated, like those of a Shortfin Mako or Lemon Shark. In the Shortfin

Mako (fig. 2.25), the teeth are directed rearward, preventing any prey unlucky enough to be captured from getting away. Both species of frilled sharks (Frilled and African Frilled) have recurved teeth like those of a python, and there are about 300 of these rearward-pointing, interlocking teeth in about 25 rows! If a prey item is unfortunate enough to be grasped by a frilled shark, there is no way it can escape. Noted shark biologist Dean Grubbs once required assistance to remove his hand from the mouth of a Frilled Shark (*Chlamydoselachus anguineus*), a *dead* Frilled Shark.

Some sharks and rays, such as the Tawny Nurse Shark (*Nebrius ferrugineus*), Mexican Horn Shark (*Heterodontus mexicanus*), and Cownose Ray (*Rhinoptera bonasus*), include shelled prey like scallops, clams, snails, crabs, sea urchins, and others in their diet. Feeding on hard-bodied prey like these is known as *durophagy* (*dur* = hard; *phag* = eating). It is not surprising that durophagous sharks and rays do not require teeth that tear or snag, but rather teeth that are broader and smaller, and in some cases these teeth are organized into crushing plates.

In many sharks, the teeth in the upper and lower jaws differ. In the Caribbean Reef Shark (*Carcharhinus perezi*) and related species, including the Galapagos (*Carcharhinus galapagensis*), Sandbar, and Dusky (*Carcharhinus obscurus*) Sharks, among others, the teeth in the lower jaw grasp while those in the upper jaw slice.

In addition to formidable teeth, the way a mouth can move impacts biting ability. *Jaw suspension* refers to how the upper and lower jaws connect to the skull and other supporting structures. To get an idea of the importance and role of jaw suspension, place an apple in a big bucket of water and try to pick it up using only your mouth (no hands!), an activity called bobbing for apples. Bobbing for apples is not easy for humans, or indeed any terrestrial vertebrate, because our upper jaw is firmly affixed to our skull. This condition works for you (except when bobbing for apples), given your evolution as a consumer of food on land. But would this type of jaw-skull connection work for an aquatic predator like a shark? No. The restricted mobility of your human jaw—that is, its inability to protrude—combined with a small gape (opening), limits the scope of your diet. Can you imagine a shark with a jaw like yours, needing to continuously reposition itself so that its very small mouth was in the right place to catch and bite a prey item in the water? If that were the case, we would very likely be discussing sharks as a minor group or even in the past tense, as evolutionary experiments gone bad—dead ends.

How then is the jaw suspension of sharks different from yours? Although there is variation among distinct groups of sharks, the most

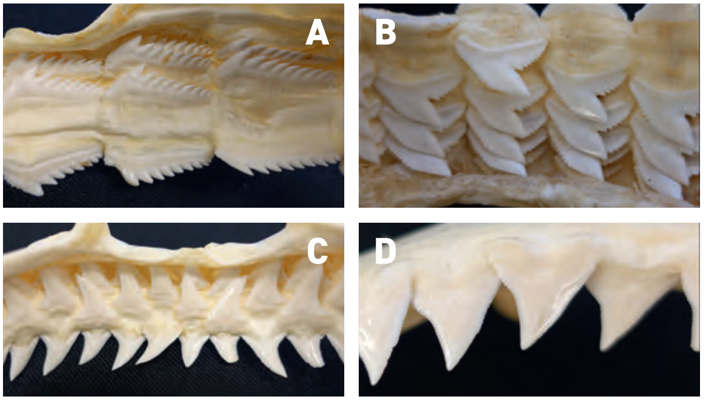


FIGURE 2.17 Teeth diversity in sharks. (A) Bluntnose Sixgill Shark (*Hexanchus griseus*), (B) Tiger Shark (*Galeocerdo cuvier*), (C) Blue Shark (*Prionace glauca*), (D) Bull Shark (*Carcharhinus leucas*). R. Dean Grubbs

evolutionarily advanced types, like Grey Reef Sharks, Bull Sharks, and Tiger Sharks, feature a loosening of the connection between the upper jaw and the skull. This allows the jaw to protrude to varying degrees (fig. 2.3), and the shark can thus bite from a slightly greater distance. This large gape also facilitates grasping, shearing, manipulation, and ingestion of prey and has contributed immensely to the success of modern sharks.

Shark bites are among the strongest in the animal kingdom, right? Actually, while the bite force of a White or Bull Shark is high, it is in the same range as that of crocodiles, alligators, big cats, and others. The force of shark bites closely

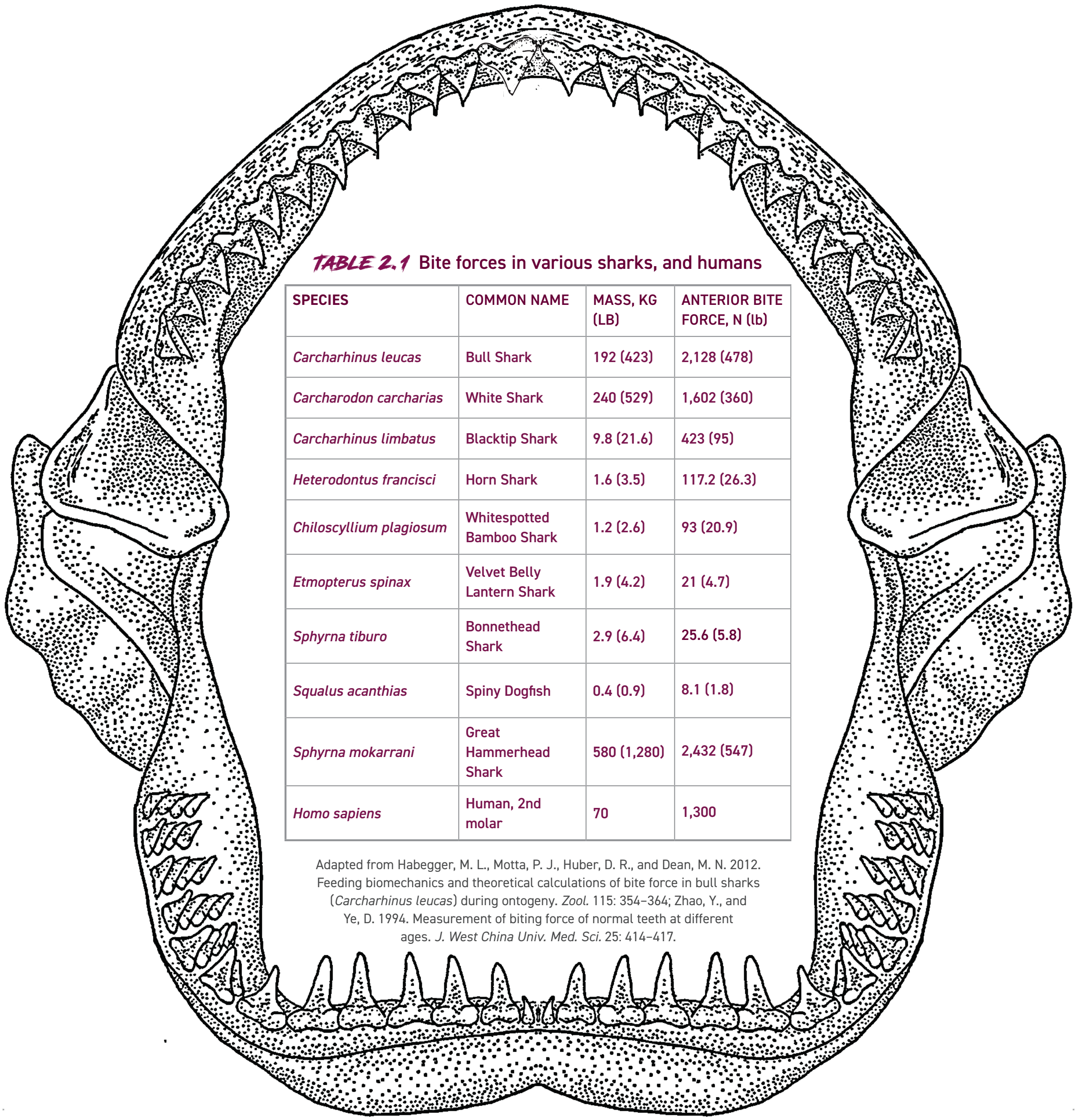


TABLE 2.1 Bite forces in various sharks, and humans

SPECIES	COMMON NAME	MASS, KG (LB)	ANTERIOR BITE FORCE, N (lb)
Carcharhinus leucas	Bull Shark	192 (423)	2,128 (478)
Carcharodon carcharias	White Shark	240 (529)	1,602 (360)
Carcharhinus limbatus	Blacktip Shark	9.8 (21.6)	423 (95)
Heterodontus francisci	Horn Shark	1.6 (3.5)	117.2 (26.3)
Chiloscyllium plagiosum	Whitespotted Bamboo Shark	1.2 (2.6)	93 (20.9)
Etmopterus spinax	Velvet Belly Lantern Shark	1.9 (4.2)	21 (4.7)
Sphyrna tiburo	Bonnethead Shark	2.9 (6.4)	25.6 (5.8)
Squalus acanthias	Spiny Dogfish	0.4 (0.9)	8.1 (1.8)
Sphyrna mokarrani	Great Hammerhead Shark	580 (1,280)	2,432 (547)
Homo sapiens	Human, 2nd molar	70	1,300

Adapted from Habegger, M. L., Motta, P. J., Huber, D. R., and Dean, M. N. 2012. Feeding biomechanics and theoretical calculations of bite force in bull sharks (*Carcharhinus leucas*) during ontogeny. *Zool.* 115: 354–364; Zhao, Y., and Ye, D. 1994. Measurement of biting force of normal teeth at different ages. *J. West China Univ. Med. Sci.* 25: 414–417.

matches what they need in order to grasp and hold on to their prey, or to take out a chunk of flesh. Our expectation of extremely high bite forces is based on continuous media reinforcement of that perception, or our belief that sharks simply look like they should have high bite forces. Recent studies have provided estimates of anterior bite force (at the front of the jaws) for several species, shown in table 2.1

Surprisingly, in some species such as the Tiger Shark and cow sharks, the jaw cartilages are weakly calcified and bend easily, and thus they do not generate the expected high bite force. Therefore, the dried jaw of a Tiger Shark is usually deformed compared to that of, say, a Bull Shark. The weak calcification permits the jaws to bend across the surface of prey (e.g., sea turtles in the case of Tiger Sharks), thus allowing most of the functional teeth to make contact. Shaking the head or rolling the body removes large chunks of flesh from the prey.

How high are bite forces of durophagous species, those that eat hard prey and typically possess large jaw musculature (fig. 2.18) and teeth designed for grinding? Anterior bite force for a 3.5 lb (1.6 kg) Horn Shark is only 26.3 lb (117.2 N), but maximum bite force on the posterior molars is 76 lb (338 N). These numbers seem low compared to measurements for Bull and White Sharks, but relative to the shark's size, they represent one of the highest bite forces among sharks.

HOW ARE SHARKS DOING?

Such fearsome predators must rule the sea, right? So how are sharks doing? There is both good and bad news about the status of shark populations. The good news is that more people and governments are beginning to appreciate the intrinsic, ecological, and even financial value of sharks in their habitats, more than as food or products. This has led to effective, science-based management of some species, including designation of some areas (e.g., the Bahamas and Palau) as shark sanctuaries.

But there is plenty of bad news. First, policy makers do not know as much as they need to about the life history characteristics of most

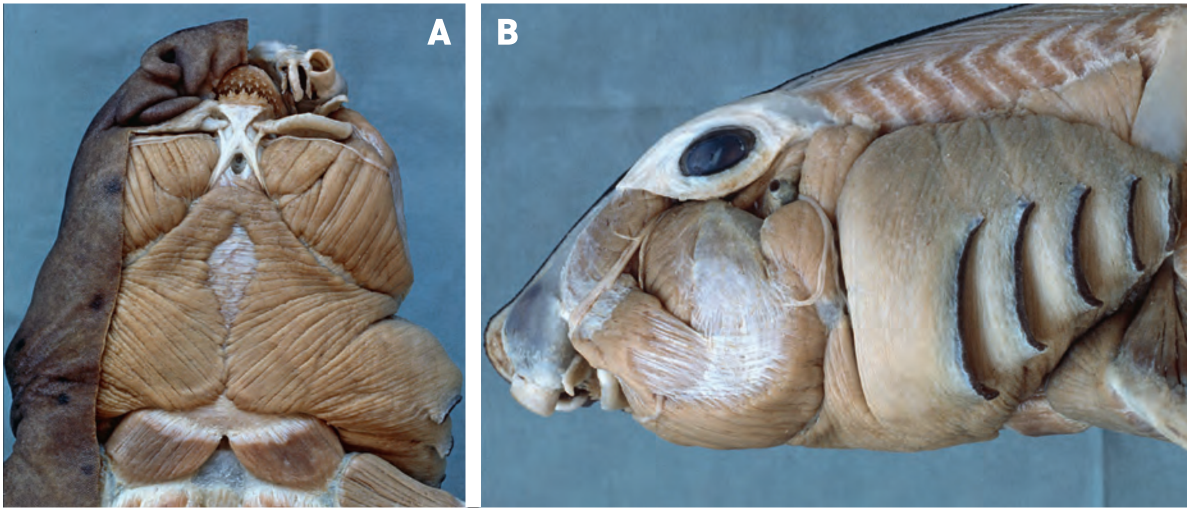


FIGURE 2.18 (A) Ventral view of a Horn Shark (*Heterodontus francisci*) showing hypertrophied jaw musculature used to crush hard prey. (B) Side view of Horn Shark. Physiological Research Lab, Scripps Institution of Oceanography

sharks in order to effectively conserve them, especially those in the deep sea. Nor do scientists understand with any degree of precision the health, behavioral, and ecological impacts on sharks of many environmental threats. What we do know is that removing them from an ecosystem causes changes, although accurately understanding those changes is not easy. But a reef with a healthy shark population is an ecologically healthier place than one without sharks.

Sharks, even those whose populations are stable, live in an ocean imperiled by human-caused climate change that is warming and acidifying their environment, with repercussions for every aspect of their biology and ecology. Also, even if sharks are protected, in many areas enforcement of regulations may be limited or absent. One of the biggest current threats to sharks is overfishing. Sharks are caught for their meat, fins, liver, cartilage, skin, teeth, and jaws, as well as other body parts. Live sharks are captured for use in aquaria. They also serve as ecotourism draws.

Since the 1980s, shark fins (fig. 2.19) have been the most economically valuable part of the shark and are still one of the most profitable, after shark meat. They are used mostly for shark fin soup, which is considered a delicacy and status symbol in countries in East and Southeast Asia. All fins on a shark are used except the upper lobe of the caudal, where the vertebral column extends all the way to the tip.

It is important to distinguish between illegal finning and the legal shark fin trade. The former involves removal of the fins from a shark, most often immediately upon capture when the animal is still alive. The now less valuable, finless, dying shark is then thrown back into the water. The legal shark fin trade involves fins from legally caught sharks that are typically brought back to port whole and are used for meat and other products. Numerous countries[9] have various kinds of restrictions or bans on finning or on shark fin soup.

Peak global value for the shark fin trade was about US$300 million in the early 2000s. Hong Kong is still the world's biggest trader of shark fins, with about 40%–50% of the global total, followed by Trinidad and Tobago. Commercial fishers from Spain and Indonesia are responsible for the largest shark catches for the shark fin industry. In the

FIGURE 2.19 (A) Shortfin Mako (*Isurus oxyrinchus*) and (B) Blue Sharks (*Prionace glauca*) with fins removed in a market in Cádiz, Spain.

United States, there is a legal shark fin trade. If shark fisheries are allowed, it seems likely that fins will be traded so that as much of the carcass as possible is used. How do you feel about this policy?

Shark cartilage is widely used as a health supplement, although the health benefits are not supported by sound, science-based evidence. The claims include protecting against or curing eczema, ulcers, hemorrhoids, arthritis, and other diseases and disorders, most notably cancer. Sharks can develop cancer, and no reputable studies have shown that eating their cartilage will protect you from it.

Shark jaws and teeth, as well as preserved shark embryos and juveniles, are bought and sold at trade shows and markets and online. All are legal to purchase, except those from species like sawfish and others that are on the US endangered species list or are present in Appendix I of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora), which prohibits their trade.

As a group, shark and ray fisheries represent less than 1% of the total marine capture fishery. The top five countries with the highest landings of sharks and rays are India, Indonesia, Mexico, Spain, and Taiwan. These five plus Argentina, the United States, Pakistan, Malaysia, and Japan are responsible for about 60% of the shark and ray landings worldwide. The remaining 40% are from small countries, mostly island nations or poorer countries in Africa, and mostly from artisanal fisheries, which, as we stated above, are difficult to get good data from. This remains a vexing problem.

Bycatch—that is, catch of nontargeted species—impacts shark populations and complicates managing them (fig. 2.20). Sharks constitute bycatch on most fishing gear, including longlines, trawls, and gill nets. High-seas drift gill net fisheries, such as those for squid and salmon in the North Pacific, have large shark bycatch. Purse seining for tuna also entails considerable bycatch. In New South Wales, Australia, declines of more than 90% were seen in a large suite of deep-sea sharks between the late 1970s and the late 1990s as the result of bycatch in a deep-sea trawl fishery. Ghost fishing gear—that is, hooks and nets that are lost or abandoned—also causes mortality in sharks (and other endangered taxa like marine mammals, seabirds, and sea turtles).

FIGURE 2.20 Dead Greenland Shark (*Somniosus microcephalus*) on the deck of a bottom trawler in the North Atlantic. Juan Vilata/Shutterstock

Mortality rates for shark bycatch vary with the species and method and can be substantial. On pelagic longlines, some sharks, such as Smooth (*Sphyrna zygaena*), Scalloped, and Great Hammerheads (*Sphyrna mokarran*), as well as all the threshers, suffer mortality rates of at least 25% and sometimes more than 50% before being boated. It is likely that most of the sharks released alive in this fishery do not survive. In contrast, the mortality rate of Blue, Silky, and Oceanic Whitetip Sharks—the three species most often caught on pelagic longlines—as well as the makos, is only 5%–20% when landed, and the few data available suggest that survival after release may be quite high. We know little about the survival rates of deep-sea sharks released after capture, but the evidence suggests, particularly for small species, that very few survive, even if they are released relatively unharmed.

Globally, sharks are protected by several agreements, including CITES, an agreement currently between 183 governments. Also, the IUCN (International Union for the Conservation of Nature) Shark Specialist Group prioritizes species at risk, monitors threats, and evaluates conservation action. The Memorandum of Understanding on the Conservation of Migratory Sharks, an environmental treaty of the United Nations, includes 40 species of sharks and rays.

In federal waters of the United States—that is, from 3 to 200 mi (5–300 km) from shore—the primary law governing fisheries management is the Magnuson-Stevens Fishery Conservation and Management Act. Within three miles of shore, management of marine resources is in the jurisdiction of states, which typically work closely with federal managers. The major means by which fisheries are regulated are Fishery Management Plans (FMPs), which assess the health of the stock in question and then establish scientifically sound regulatory measures. Currently, US Atlantic sharks (classified as *large coastal sharks*, *small coastal sharks*, or *pelagics*) are under management. By 2016, large coastal sharks were managed at a quota that was 8% of historical peak landings, and the most vulnerable species remained prohibited. Because the Spiny Dogfish stock apparently recovered, landings in this fishery increased, making up 39% of the 2016 commercial landings. They are now often commercially called Cape Sharks, apparently a more a palatable term for consumers than "dogfish." (Although we eat catfish, no?) Sandbar Sharks are on a trajectory to recover in the second half of the twenty-first century, several decades away. Dusky Sharks remain one of the most overfished sharks on the US East Coast, and their full recovery is not expected until after 2100. 2100! Do not eat sharks unless you know they are part of a sustainable fishery!

Along the US West Coast, sharks are managed under the Fishery Management Plan for West Coast Fisheries for Highly Migratory Species. Managed species include all three species of thresher sharks, Silky Sharks, Oceanic Whitetip Sharks, Blue Sharks, both species of makos, and the Salmon Shark (*Lamna ditropis*).

Outside the United States, sharks are managed by a variety of methods, although in the United States as well as in other countries, enforcement remains an issue. A growing number of countries (16 as of 2022) have declared their territorial waters to be shark sanctuaries to reduce shark mortality and aid in their conservation.

While targeted fisheries and bycatch are considered the principal current dangers for sharks, climate change, habitat degradation and destruction, pollution (nutrient pollution from agricultural runoff and undertreated human sewage, plastic pollution, and other chemicals), exotic introductions, and aggregated human disturbance (persecution, noise pollution, etc.) are also major threats. The short- and long-term

FIGURE 2.21 (A) Sandbar Shark (*Carcharhinus plumbeus*) with plastic strap encircling its body, caught on an experimental longline. (B) Same shark being successfully released after the strap was removed. It swam away strongly. George Boneillo

impacts of these threats on sharks are not all known. They may be minimal, or they could range from sublethal impacts that affect an organism's overall fitness (e.g., its internal functions and behavior) to mortalities that cause declines in populations. Here, we briefly consider plastics, habitat degradation, and climate change as examples of the threats sharks face.

Figure 2.21 shows a Sandbar Shark we caught on an experimental longline in 2016 in Winyah Bay, South Carolina, with a plastic packaging strap fully encircling the shark near the gills. This shark likely survived after we removed the strap, since it appeared otherwise healthy, was actively feeding (it took the bait on our longline), and swam off strongly once released, but many sharks and other marine life do not survive similar entanglements.

Plastic is so commonplace that we are said to be in the Age of Plastics. Estimates of the amount of plastic that finds its way into the marine environment annually range from 1.8% to 10% of annual global plastic production. Once in the marine environment, plastics cause a suite of problems at the organismal and ecosystem level, although much remains to be understood about these impacts. Broadly, sharks are affected by plastics through entanglement or ingestion. Entanglement of sharks in plastics has been reported anecdotally (as in our example above), especially from abandoned drift nets. However, the global extent of entanglement and its impacts on local populations and ecosystems are difficult to assess.

Ingestion of plastics has been studied more rigorously than entanglement and is a major line of inquiry as we write this book. Direct ingestion of large plastic by sharks seems rare, but smaller pieces are routinely swallowed. As of 2021, sharks found with ingested microplastics included 15 species, but the number will assuredly expand as more sharks are examined.

Microplastic (< 5–10 mm, or 0.2–0.4 in) toxicity may result either from adsorption of harmful chemical pollutants to the surface of the microplastics, such as PCBs, DDE, and DDT, or from additional harmful chemicals in the plastics, such as flame retardants and plasticizers. However, studies on the effects of toxic microplastics on sharks, as well as other species, are lacking. Additionally, although the subject has not yet been thoroughly studied, evidence suggests that plastics can move up the food chain.

Let us look at mangroves as an illustration of the problem of habitat degradation. Mangroves, one of the most biologically productive ecosystems on the planet, are a broad group of salt-tolerant trees that grow at the water's edge in the tropics. They play important roles in the life histories of numerous sharks as well as critically endangered rays, like the sawfish. Stilt roots of mangroves at the water's edge provide myriad hiding places for a great diversity of marine life, especially the juvenile and larval forms of fish, crustaceans, and mollusks, any of which constitute food for sharks. They also provide nursery habitat for some shark species. Mangrove communities are at high risk from development, especially in countries with few if any land-use controls. Mangrove environments are readily cleared for aquaculture, resort developments, and housing. They are also threatened globally by rapid sea-level rise and locally by agricultural runoff, oil, deforestation for biomass fuel, and gas exploration and production.

Already, as much as 50% of the world's mangroves have been lost, and more have been degraded by pollution. And mangroves also serve as important buffers against coastal storms for humans in the vicinity, so it is not just sharks we are putting at risk. One particularly well-researched species is the Lemon Shark of Bimini, Bahamas (fig. 2.22). Mangroves and the lagoons fringed by the mangroves are critical to the growth and survival of juvenile Lemon Sharks during their first few years of life, after which they move to more nearshore or coastal habitats. Young Lemon Sharks take advantage of the protection from predation offered by the mangroves (mainly from larger Lemon Sharks), as well as the abundant food supply in the lagoon.

By 2010, development of a resort in Bimini, Bahamas, had involved dredging and removal of about 166 ac (67 ha) of mangroves, representing 39% of the mangrove habitat surrounding the

FIGURE 2.22 A juvenile Lemon shark (*Negaprion brevirostris*) patrols the mangroves in Bimini, Bahamas. Annie Guttridge

system. This habitat was one of the most important Lemon Shark nurseries in the northwestern Bahamas, which also serves to recruit adult Lemon Sharks to southeastern US habitats. After the development started, survival rates and growth rates of Lemon Sharks both decreased, and sharks remaining in the area were less healthy than comparable sharks in undisturbed areas. Clearly the sharks, and undoubtedly their marine neighbors, need minimally degraded coastal habitats.

What are some of the impacts of climate change on sharks? Let us start with acidification and temperature, although since climate change will affect both these variables, separating acidification from temperature changes may produce conflicting and confounding results. The scale of impacts of ocean acidification has the potential to be enormous, causing changes in ocean chemistry that have not been seen in 65 million years, which will affect the vitality and survival of all taxonomic groups. Impacts of acidification on sharks may be direct, such as affecting internal function (by acidifying blood and tissues) and behavior of sharks, or indirect, such as changing the community structure or prey. As of 2022, few studies of the effects of acidification on sharks have been published. Like many other shark studies, these have focused on smaller species, particularly benthic sharks, that are most readily maintained in captivity and are thus not applicable to the group as a whole. They suggest decreases in resilience and fitness as acidification increases. In a study of behavioral responses to acidification, Port Jackson Sharks took about four times longer than control sharks to detect their prey in acidified water. However, that time was reduced by a third when the study was conducted in water that was warmer than normal. Dusky Smoothhounds in a different study exhibited an impaired ability to track prey using odors in acidified water.

Temperature is one of the most significant environmental influences on organisms. In contrast to studies of acidification effects, there are many studies on the effects of elevated temperature on this group, such as signals for movements, as well as impacts on behavior, respiration and metabolism, growth, swimming, reproduction and embryonic development, and foraging. However, fewer of these have focused on warming in the range associated with human-caused climate change, and thus it is too early to conclude with confidence what the specific impacts of temperature changes, especially increases, are on sharks.

Some additional climate change impacts that could affect sharks include changes in precipitation patterns that alter the salinity structure of nearshore and oceanic systems, increased intensity and frequency of tropical storms, and rising sea levels that coastal wetland communities may not be able to keep up with. Also, larger and more severe oceanic dead zones occur because of oxygen depletion triggered by excess nutrient runoff, often adjacent to the mouths of major rivers. Some of these impacts may occur on an even larger scale, such as changes in ocean circulation that could include a critical slowing of the Gulf Stream, a current that moderates temperatures along the entire coast of North America over to Europe.

What would be the ecological impacts of these changes? Many sharks and rays would be forced to migrate to higher latitudes or deeper water because of temperature increases. For example, a 2018 study[10] showed the presence of juvenile Bull Sharks in North Carolina estuaries, which had not previously been a frequently used habitat, and correlated their presence with the early arrival of summer temperatures. In moving to higher latitudes, sharks and rays may encounter ecosystems novel to them. These may cause problems like changes in the abundance and size structure of shark populations; changes in the food chain; changes in behavior; and possibly mortalities, extirpations, and even extinctions of species for which migrations may be difficult or improbable or which may already be depleted or threatened by other stressors.

Sharks have an evolutionary history reaching over 400 million years, but are they capable of surviving the current human-dominated era, the Anthropocene, and the sixth mass extinction we are causing? The most recent assessment by the IUCN is not optimistic. A comprehensive evaluation of sharks, rays, and chimaeras (all closely related cartilaginous fish) published in 2021 found that 37% of species for which sufficient data exist are threatened with extinction.

A FEW OF THE APEX PREDATORS AMONG SHARKS

WHITE SHARK
(Carcharodon carcharias)

What can we say about one of the most iconic species on the planet (fig. 2.23)? Is it overrated? Well, if overrated means that the species receives

FIGURE 2.23 White Shark (*Carcharodon carcharias*).
Tanya Houppermans

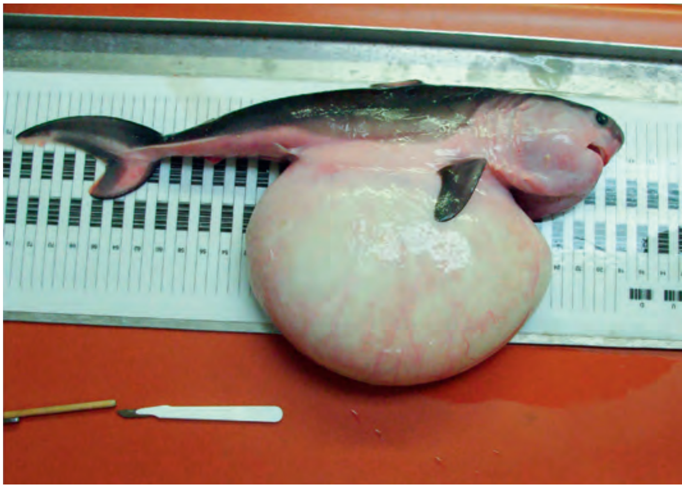


FIGURE 2.24 Embryo of a Salmon Shark (*Lamna ditropis*), a close relative of the White Shark and makos, exhibiting its yolk stomach filled with ova it has consumed while developing in the uterus.
Kenneth J. Goldman, PhD

attention disproportionate to its ecological importance or conservation status, often to the exclusion of more interesting and endangered sharks, then yes. On the other hand, if caring about this species leads to awareness of the plight of other sharks and inhabitants of the planet in general, and thus valuing our natural environment, then no.

White Sharks and Shortfin Makos are among the five species of mackerel sharks (family Lamnidae), all of which are high-performance predators with a large, fusiform (spindle shaped, or tapering at both ends) body as long as 13–20 ft (4–6 m), a crescent-shaped caudal fin, and a pointed snout. They also maintain their body temperature above that of the water in which they reside, as we described earlier. All are pelagic, typically at 490–3,280 ft (150–1,000 m) in most temperate and some tropical seas. As embryos, mackerel sharks grow and mature in their mother's uterus by eating the unfertilized ova the mother continues to produce, and they develop very cute pot bellies, more commonly called egg, or yolk, stomachs (fig. 2.24).

Characteristics of White Sharks include their large size (up to 20 ft, or 6.1 m, and 4,200 lb, or 1,900 kg), a jaw full of triangular serrated teeth for cutting, long gill slits, vivid color changes on the sides, and black tips under the pectoral fins. The species is globally distributed in both coastal and oceanic waters where the temperature is 54–75°F (12–24°C). Contrary to the public's perception, the overall population is not declining and in fact has been increasing in many regions during the last 20 or 30 years, although optimism must be tempered against the reality of a critically imperiled ocean, as well as population decreases in some locations.

Their diet consists of marine mammals (seals, sea lions, elephant seals, and dolphins) as well as bony fish, sharks, and rays. They will also feed opportunistically on whale carcasses. White Sharks may also occasionally eat sea turtles. Neonates and smaller juveniles consume mostly fish. We would be remiss not to mention the acrobatic, aerial predatory behavior of White Sharks at Seal Island, South Africa. While breathtaking complete breaching may occur, the repertoire of predatory activities of these White Sharks includes a suite of behaviors (e.g., broaching and lunging) that are employed in preying on Cape Fur Seals.

The White Shark is perpetually in the news, but recent reports merit particular attention in a book about predators. First near Southeast Farallon Island, south of San Francisco, and more recently off South Africa, are reports of White Sharks being killed by Orcas, which apparently removed the liver and possibly other internal organs. Even if this activity is novel, that Orcas may have enlarged their range of prey to include White Sharks would not be an unusual feat for so intelligent and, well, predatory an animal.

SHORTFIN MAKO
(Isurus oxyrinchus)

This species is perhaps the most magnificent fish in the sea (so says a shark biologist), with its beautiful coloration (brilliant blue or purple on top, white on the bottom) (fig. 2.25) and its near perfect streamlining. It is found globally in temperate and tropical waters.

Distinguishing features include a conical snout, moderately short pectoral fins, crescent-shaped tail, dagger teeth, and huge gill slits. They grow to at least 14.6 ft (4.45 m). They eat mainly bony fish and squid, often swallowing them whole, and are considered opportunistic apex predators. As they age, their teeth become broader and flatter, enabling them to widen their prey options to include organisms too large to swallow whole but from which they can remove a chunk of flesh, such as swordfish, tuna, sharks, sea turtles, and marine mammals. Specimens have been captured or observed with swordfish bills impaled in their head region and even their vertebral column. Sometimes dinner fights back.

The Shortfin Mako is considered Vulnerable in the Atlantic and Indo-West Pacific, and Near Threatened in the eastern North Pacific.

TIGER SHARK
(Galeocerdo cuvier)

Found worldwide in tropical and temperate coastal waters, this iconic, large shark (16.5 ft, or 5.0 m) is easily identified by its markings, which are most vivid in juveniles; its long caudal fin; and its wide, multicusped teeth (fig. 2.26). Like the cow sharks, Tiger Sharks have surprisingly relatively weak jaws that bend across the body of large prey (e.g., sea turtles, dead whales). They then twist or spin their bodies to carve out huge chunks of flesh.

Tiger Sharks may produce 60 or more pups every three years. Because of their high reproductive potential, Tiger Shark populations are considered healthy globally. However, a recent study showed a 71% decline in Tiger Sharks along the east coast of Australia.[11]

While Tiger Sharks have virtually no predators as adults, in some locations they eat lower in the food web, since the food item they frequently consume, sea turtles, eats primarily plants.

▲ FIGURE 2.25 Shortfin Mako (*Isurus oxyrinchus*). Wildestanimal/Shutterstock.com

▼ FIGURE 2.26 Tiger Shark (*Galeocerdo cuvier*). Ken Kiefer

BULL SHARK
(Carcharhinus leucas)

This is a stout shark with a robust, blunt, rounded snout (fig. 2.27). It has a large first dorsal fin situated far forward on its body. Its eyes are relatively small, but its teeth are broad and heavily serrated for shearing.

The Bull Shark is found predominantly in shallow tropical and temperate waters less than 100 ft (30 m) deep, but it can be found shallower and as deep as 538 ft (164 m). It is considered

FIGURE 2.27 Bull Shark (*Carcharhinus leucas*). Ken Kiefer

dangerous, especially in the developing world where the daily lives of inhabitants find them in Bull Shark habitat, particularly brackish and fresh waters. When Bull Sharks encounter a boat in shallow, clear tropical waters, they may go into a threat display, lowering their fins and hunching their back. When they do that, they may charge and strike the boat. Try not to fall in right then!

Bull Sharks eat a variety of bony fish as well as sharks and rays (see fig. 2.2B). Their occasional prey includes sea turtles, dolphins, seabirds, crustaceans, and squid.

SANDBAR SHARK, BROWN SHARK *(Carcharhinus plumbeus)*

The Sandbar Shark is distributed worldwide and is an ecologically important, bottom-dwelling species of coastal temperate waters shallower than 330 ft (100 m) (fig. 2.28). In many ecosystems it shares the top spot in the food web with other sharks or is one level lower; in other words, it is not always an apex predator. The Sandbar Shark reaches a maximum length of 8 ft (2.4 m). It has an oversized first dorsal fin far forward on its body. The Sandbar Shark is the dominant shark along the US East Coast as well as in Hawai'i, but it occupies deeper water in the latter. The biggest Sandbar Shark nursery in the world—that is, the area where they are born and/or spend their early years—is Chesapeake Bay. In large part because of their large first dorsal fin's value to the shark fin soup industry, Sandbar Sharks drove the US East Coast shark fishery until they became overfished. They are no longer overfished, but full recovery is not expected for decades.

The Sandbar Shark is a generalist when it comes to feeding. Its diet includes bony fish, crustaceans, mollusks, and other invertebrates.

OCEANIC WHITETIP SHARK *(Carcharhinus longimanus)*

The common name describes the prominent edges of the fins, which appear to have been dipped in white paint (fig. 2.29). The Oceanic Whitetip Shark is a stocky, large (to at least 11.5 ft, or 3.5 m), pelagic shark found in temperate and tropical oceans. It has a reputation of being aggressive and dangerous. This reputation is exaggerated, but the Oceanic Whitetip Shark is inquisitive; it will likely bump people it encounters and may bite, and thus caution is always advised when diving with this species. It is considered Vulnerable by the IUCN.

Oceanic Whitetip Sharks eat mainly bony fish (e.g., marlin, tuna, mahi mahi, mackerel), sea turtles, seabirds, squid, and crustaceans. Like other pelagic sharks, they will also opportunistically feed on whale carcasses.

GREAT HAMMERHEAD
(Sphyrna mokarran)

The Great Hammerhead is one of nine species of hammerheads. The first dorsal fin is enormous, and there are large pelvic fins as well as a huge upper caudal fin (fig. 2.30).

FIGURE 2.28
Sandbar Shark (*Carcharhinus plumbeus*). Brandon B / Shutterstock.com

FIGURE 2.29
Oceanic Whitetip Shark (*Carcharhinus longimanus*), a ridgeback species. Ken Kiefer

Great Hammerheads are found in all tropical and warm temperate seas in both inshore and pelagic environments, from the surface to 987 ft (300 m). They reach a length of 20 ft (6 m). They feed on fish, including rays. Their weird head, called a *cephalofoil*, may play roles in both maneuverability and stability. It may also be used for prey handling by pinning rays to the bottom before eating them.

The Great Hammerhead is considered Critically Endangered. Capture mortality is very high in this species; capture prohibitions are therefore ineffective in curbing mortality in a multispecies fishery. A recent study showed that 50% of hammerheads were dead after three hours on the hook.[12]

Great Hammerheads eat a variety of bony fish, as well as other sharks and marine invertebrates. They also prey on rays.

BLUNTNOSE SIXGILL
(Hexanchus griseus)

The Bluntnose Sixgill is a member of a primitive group of five species of cow sharks (fig. 2.31). These are widely distributed, big (to 16 ft, or 5 m), stout-bodied predators with surprisingly weakly calcified jaws. This may be explained by problems depositing calcium salts at the depths at which they spend much of their time. Their odd, cockscomb-shaped teeth are like miniature saw blades, and the additional flexibility of the weakly calcified jaws allows the jaws to bend as they encounter prey, which includes small and large bony fish and sharks, bringing more of the serrated teeth in contact with the flesh, which is then more easily sliced and removed: death by a thousand cuts!

Most live in deep water (1,000–3,300 ft, or 300–1,000 m), a section known as the oceanic *twilight*

OPPOSITE PAGE:
FIGURE 2.30 Great Hammerhead (*Sphyrna mokarran*) in Bimini, Bahamas. Note the tight turning radius, enabled in part by the use of the laterally expanded head as a rudder. Annie Guttridge

TIHS PAGE:
FIGURE 2.31 Bluntnose Sixgill Shark (*Hexanchus griseus*) in Exuma Sound, Bahamas, photographed from a submersible. Spear guns used to tag sharks from the submersible are shown. R. Dean Grubbs

zone, but they may be shallow in some locations. They have a single, spineless dorsal fin set far back along the body, which reduces friction and allows them to spin more easily when sawing chunks of flesh from prey. They also have retractable eyes; four muscles contract and basically suck the eyeball back into its socket for protection from struggling prey.

SMALLTOOTH SAWFISH
(Pristis pectinata)

The Smalltooth Sawfish is a ray, but recall that the rays are the closest relatives of the sharks, and both are cartilaginous (fig. 2.32). Rays split off from the shark lineage about 270 million years ago. The Smalltooth Sawfish looks like a shark, and in its habitat, where it eats bony fish and other sharks, it occupies a high trophic level, which is why we include it here. Rays can be distinguished from sharks in that the pectoral fins of the former are connected to the body above the gills, which are on the ray's underside.

Smalltooth Sawfish can reach lengths of more than 16 ft (5 m). The most recognizable characteristic is the saw, or rostrum, which is basically the snout projected as a stout, thin blade, with a series of pointed teeth on both sides. The ampullae of Lorenzini, organs sensitive to minute electrical currents, extend all way to the end of the rostrum. The saw is used to probe the bottom for benthic prey and to slash and disable schooling fish.

This critically endangered species is found in tropical and subtropical coastal areas on both sides of the North Atlantic, but it has been extirpated from several areas, especially in the eastern North Atlantic. It was placed on the US endangered species list in 2003. Continued threats include coastal development, dredging, mangrove removal, seawall construction, alteration of freshwater flow, habitat fragmentation, climate change, and especially commercial fishing as bycatch. Extensive efforts to reverse population declines in southwestern Florida are beginning to work.

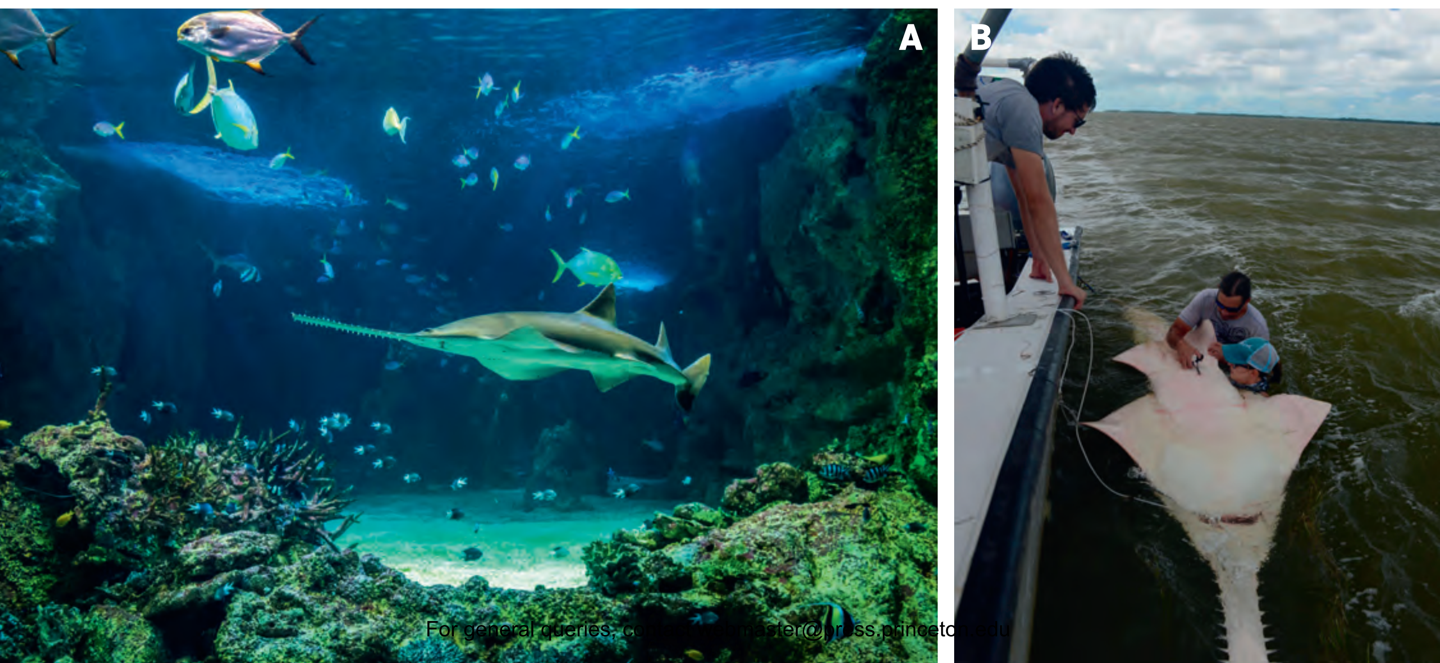


FIGURE 2.32 (A) Smalltooth Sawfish (*Pristis pectinata*) at an aquarium. (B) Scientists implanting an acoustic tag through a small surgical opening in a Smalltooth Sawfish. This will enable them to track the animal to determine its preferred habitat and movements. (A), Nick Fox / Shutterstock; (B), R. Dean Grubbs

3 NONAVIAN REPTILES

You probably learned what reptiles are in elementary school: animals that live mostly on land, have scales, and, for turtles, possess shells. Well, things change. Powerful methods for understanding relationships of all organisms using the structure of their genetic material, specifically their mitochondrial and/or nuclear DNA or RNA, have revolutionized the fields of systematics and taxonomy. Earlier taxonomists (and your teachers) weren't wrong about reptiles, but there is a somewhat surprising complication. If you look at the family tree that includes both traditional reptiles and birds (fig. 3.1), you see that the classical interpretation of what is designated as a reptile doesn't make much sense.

Either crocodylians (alligators, crocodiles, caimans, and the Gharial, as opposed to the crocodilians, which are just the crocodiles), which resemble lizards but share a more recent common ancestor with birds than with other reptiles, should be considered "birds" too, or birds should be considered "reptiles." In fact, paleontologist Robert Bakker wrote in *The Dinosaur Heresies* in 1986, "When the Canada geese honk their way northward we can say: 'The dinosaurs are migrating, it must be spring!'" We like that interpretation a lot, but it hasn't caught on yet. One solution is to continue to call birds "birds," or even "avian reptiles." Nobody we know commonly calls a hummingbird or eagle an avian reptile, but if taxonomists adopted that nomenclature, the remaining reptiles could then be referred to as "nonavian reptiles." That is where our chapter title comes from, but for convenience we will refer to these as just reptiles, as long as you, faithful reader, understand our basis for doing so.

You may have noticed we skipped from sharks to reptiles, ignoring amphibians, including the Cane Toad (*Rhinella marina*), a predator worthy of our attention, if not one that inspires night sweats. Amphibians descended from a Paleozoic group of semiaquatic ancestors. Most species still live part of their lives in the water and part on land (*amphi* = both, *bio* = life), and they all need to stay at least damp. If you value necks, lungs, distinct feet with toes, mobile tongues, inner ears, and a skeleton robust enough to stand up without the support of water, you owe gratitude to the amphibians. All adult amphibians are carnivores, too, so like the sharks in the previous chapter, they are definitely predators!

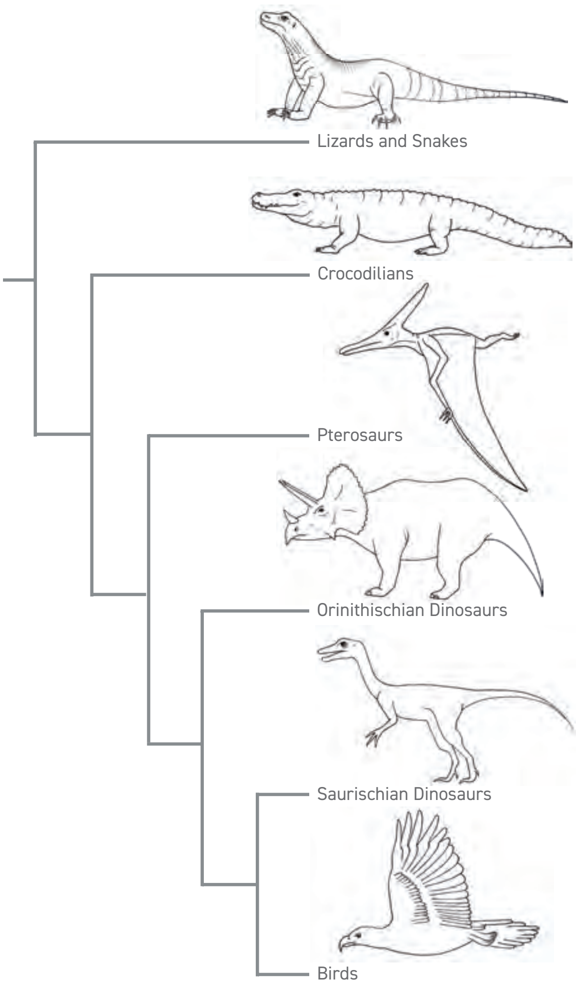


FIGURE 3.1 Reptile phylogeny. This evolutionary tree (also known as a cladogram) shows the relationships of reptiles, both avian (birds) and nonavian (classical).

The toxic Cane Toad we referenced above can weigh almost 4 lb (1.8 kg). After its ill-advised introduction to Australia in 1935, it wreaked havoc on other amphibians, reptiles (including birds), and even small mammals there. The Chinese and Japanese Giant Salamanders (*Andrias davidanus* and *japonicus*) can grow to nearly 6 ft (1.8 m) long. But these are the biggest of the amphibians and they are outliers. Most are smaller than 1 ft (30 cm). Their teeth are tiny. They are voracious consumers of insects, but with few defenses, they are prey, not top predators. As much as we love frogs, toads, salamanders, and the weird, legless caecilians, we are leaving them out.

While some of the earliest tetrapods (*tetra* = four, *pod* = foot) evolved into amphibians, others took a more terrestrial path, which meant surmounting the biggest impediment to life on land: drying out. Overcoming desiccation was a major evolutionary advancement, equivalent to the development of jaws in vertebrates. This evolutionary leap onto land required the development of a waterproof egg, "waterproofing" in this case meaning preventing fluid from leaving rather than entering. Thus, the *amniotic* egg was hatched, so to speak, with a shell that resisted water loss, which allowed it to be deposited on land and not dehydrate. Terrestrial eggs can be bigger, producing larger offspring and therefore bigger adults. Some reptiles, like many sharks, have evolved the ability to retain the eggs inside them and give birth to live young, skipping external eggs altogether. Live birth required internal fertilization, which was also required for egg layers since they could not rely on water to transport sperm to eggs. Life on land also led to the evolution of thicker skin that contained water-repelling lipids (fats) and provided protection (from parasites, predators, etc.)

The colonization of land was accompanied by problems other than desiccation. Metabolism produces ammonia, a toxic waste product that cannot be stored in the body for long. For aquatic or amphibious animals, ammonia can diffuse out or be excreted as urine. On land it must exclusively be excreted, but in such a way that conserves one of a terrestrial animal's most valuable commodities, water. Reptiles accomplish this via a complicated physiological pathway that ends with the solid *uric acid*, which can be excreted without much water. If you or your windshield have ever been pooped on by a bird, you are familiar with this white substance. Mammals produce a water-soluble relative of uric acid, *urea*, and their kidneys excrete a concentrated urine. Either way, water is conserved.

Being bigger and more active demands faster exchange of oxygen and carbon dioxide to enable the metabolic machinery to operate, and so more efficient lungs developed. The crocodylians, some lizards, and the birds have a flow-through—that is, *unidirectional*—respiratory system, which is more efficient than the tidal flow in the lungs of mammals, including you, since a fresh supply of oxygen continually courses through the lungs.

The crocodylians are the most obvious top predators among the reptiles. In fact, their ancestors were the most diverse group of meso- to top predators in the Triassic period, 200–250 million years ago (mya). They are now the largest reptiles, with large gapes and impressive teeth. Some species are less than 6.5 ft (2 m) long, but a Saltwater Crocodile (*Crocodylus porosus*) might grow to more than 20 ft (6 m) long and weigh 2,200 lb (1,000 kg). Enormous, to be sure, but not as gargantuan as *Sarcosuchus imperator* (*sarco* = flesh, *suchus* = crocodile, *imperator* = ruler) (fig. 3.2) from the Cretaceous (145–66 mya). This beast, tipping the scales at 17,500 lb (8,000 kg) and measuring 30–40 ft (11–12 m) long, lurked in African rivers waiting to ambush, well, whatever it wanted.[1] This supercroc was the size of a bus. Luckily for us, *Homo sapiens* was not around yet. However, you have probably heard of modern crocodylians eating humans or their pets, and you may have seen videos of them going after Wildebeests and zebras. Definitely top predators.

Most lizards are carnivores, but because they are not very large, they are more likely to be prey than predators. The exceptions are the Gila Monster (*Heloderma suspectum*), Mexican Beaded Lizard (*Heloderma horridum*), the tegus, and the big monitor lizards, such as the Komodo Dragon (*Varanus komodoensis*). Monsters and dragons indeed! We will talk more about these later.

FIGURE 3.2 *Sarcosuchus imperator*. This prehistoric crocodylian was as long as a school bus and weighed nearly 4 tons. Shadowgate from Novara, Italy—Museum of Natural History, CC BY 2.0, via Wikimedia Commons

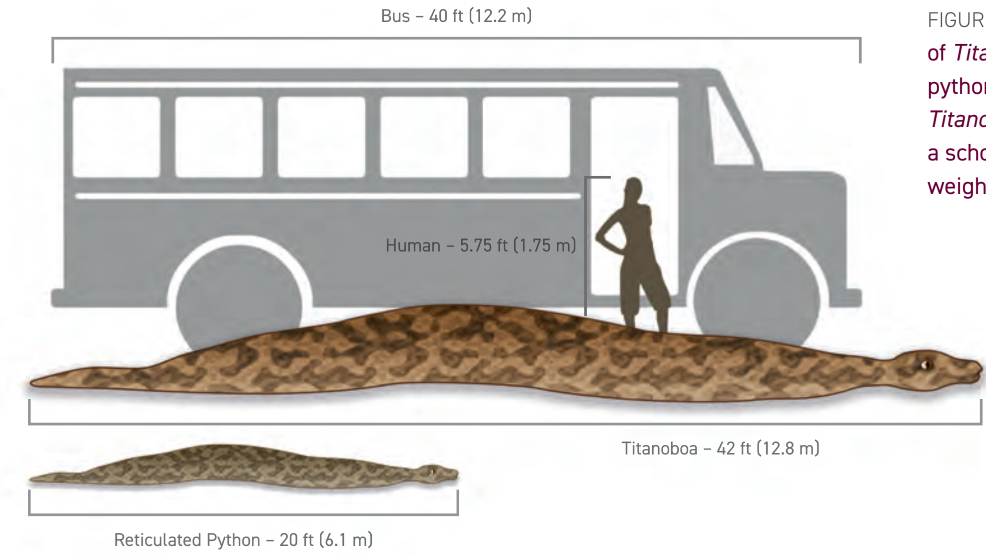


FIGURE 3.3 Size comparison of *Titanoboa* and a modern python. The prehistoric *Titanoboa* was longer than a school bus and likely weighed more than a ton.

The next reptiles that might inspire nightmares are the snakes. Snakes branched off from lizards about 128.5 mya.[2] Evolutionarily, snakes started with legs and lost them over time. For you, with legs, losing such useful appendages probably seems like a nonsensical choice, but as you will see, natural selection did not get this wrong. All snakes are predators, but few are considered top predators, although as with crocodylians there are giants in their ancestry. For example, the South American *Titanoboa* (fig. 3.3) grew to 43 ft (13 m) and weighed an estimated 2,500 lb (1,135 kg).[3] If you stood next to it, its back would reach your waist! Again, that was before the time of *Homo sapiens*. Today's closest counterpart to *Titanoboa* would be a nearly 30 ft (9 m) Green Anaconda or Reticulated Python. We will look at a couple of venomous snakes too.

Turtles typically do not inspire nightmares (except for *chelonaphobics*, people who fear turtles), but one group reaches the rarefied air of top predator, the snapping turtles. An encounter with a large snapping turtle is an unforgettable event. We will also take a brief look at those.

REPTILES AND US

Like the other beasts in this book, the crocodylians, lizards, snakes, and turtles have been and continue to be common parts of our culture. Sobek is an ancient crocodile-headed deity of ancient Egypt, representing power, protection, and fertility. Mummified crocodiles were found inside the ancient Egyptian temple of Kom Ombo. Author Roald Dahl's *Enormous Crocodile* wandered the jungle promising to eat children. If you are a fan of the University of Florida, you cheer on your Gators with an enthusiastic clapping of your arms like a snapping alligator. (Although lately you may also do this to portray a shark chomping in tune to the "Baby Shark" children's song, now the theme for the Washington Nationals baseball team in the United States—our apologies for bringing this tune to mind.)

In movies there is Ramon, from the 1980 movie *Alligator*, a mutant gator lurking in New York City sewers. The legend of gators in the sewers of New York has been around at least since a *New York Times* article describing an account of just that, published in 1935. The story really took off in 1963 with the publication of Thomas Pynchon's novel *V.*, which included a description of children all over the city buying alligators for 50 cents from Macy's, only to tire of them and flush them away, leaving alleged armies of albino alligators terrorizing sewer workers and apartment dwellers for years to come.[4]

Famous crocodylians from real life exist as well. Two-Toed Tom was a 14 ft (4 m) alligator on the border between Florida and Alabama in the 1920s. He lost all but two of his toes on one foot in a steel trap, so he was easily identified by his footprints. He evidently survived being shot and an attempt to explode him with dynamite. During this latter effort, he allegedly ate half his attacker's granddaughter, a sad ending to the story.

There is also Gustave, the Killer Crocodile of Burundi. This fellow, a Nile crocodile (*Crocodylus niloticus*), is about 20 ft (6m) long, could weigh more than a ton (900 kg), and is rumored to have killed as many as 300 people.[5] We suspect there were and are more of these legendary crocs in existence around the world because both they and people frequent rivers in Asia, Africa, and Australia and sometimes run into each other. Nile Crocodiles in Africa, the most common of the crocodylians, are estimated to kill over 300 people annually. Saltwater Crocodiles in both Australia and Malaysia round out the list of deadliest crocodylians.

Most famous lizards are actually dinosaurs, which are not lizards at all (although they are reptiles). Godzilla, for example. Not counting those, most lizards in culture are friendly pets (Ms. Frizzle, driver of *The Magic School Bus*, had one) or spokes-lizards (the GEICO insurance company gecko), and they are, well, not all that famous. Cheyenne people consider it bad luck to kill a lizard, and the Gila Monster is a powerful hero to the Navajo.[6]

The ancient Greeks viewed snakes as sacred, with the ability to shed skin a symbol of rebirth and renewal. You can be born in the Chinese Year of the Snake, which is okay, but most snakes in culture are bad guys. First, according to Judeo-Christian lore, there was that demon-snake in the Garden of Eden that ruined the whole thing by enticing Eve. Rudyard Kipling had villain Kaa in *The Jungle Book*, and Nag and Nagaina in *Rikki-Tikki-Tavi* (if you are familiar with this latter story, it is absolutely true that a mongoose is capable of killing a snake). Harry Potter's nemesis Voldemort had the giant python-viper hybrid Nagini (clearly J. K. Rowling is familiar with *Rikki-Tikki-Tavi*). Even in most Native American cultures, where animals are generally revered, the snake is associated mostly with violence, revenge, and bad luck.

Mara, a being of pure hatred in the television show *Doctor Who*, can manifest as a snake that requires fear from people to survive. This fictitious requirement succeeds in the program because many people are deathly afraid of snakes. You may recall the famous scene from the movie *Raiders of the Lost Ark*, in which our not quite fearless hero, Indiana Jones, drops his torch into a crypt, revealing a mass of squiggling serpents, and says in disgust, "Snakes. Why did it have to be snakes?" His sidekick then deadpans, "Asps. Very dangerous. You first." (The impressive piles of snakes in the pit were mostly legless lizards, which are harmless. Take a scientist with you to the movies!)

Because it is so common, fear of snakes, *ophidio-* or *ophiophobia*, has led to considerable research on whether this fear is innate or learned. The consensus now seems to be that it is both. For primates, the larger group of over 700 species and subspecies to which humans as well as monkeys and apes belong,[7] this fear is probably less innate and more learned. In evolution, primates became predisposed to notice snakes, so learning to fear them comes very easily for humans. A primate, including a human toddler, when presented with a picture of flowers with snakes hidden throughout, will immediately see the snakes.[8] This makes sense evolutionarily. If experience or a parent lets the little primate know that snakes can be trouble, and it notices them easily, then it is more likely to last long enough to reproduce compared to the primate who does not. And once you are afraid of snakes, as with all phobias it is a devilishly difficult fear to unlearn.

As for turtles, in many native creation stories it is a turtle that holds up the Earth. This is a common theme in author Terry Pratchett's *Discworld* fantasy novels, in which a disk-shaped Earth floats through space, supported on the back of four massive elephants, which in turn are supported by an enormous turtle, the Great A'Tuin. After a lecture on cosmology, nineteenth-century philosopher and psychologist William James was accosted by an elderly lady claiming she had a better theory: we live on a crust of earth that is on the back of a giant turtle. James asked what the turtle stood on. "It's turtles all the way down!"[9] Turtles are associated with long life and protection. In the Santeria religion, it is good to live with a turtle because it absorbs negative energy. If you are a Buddhist, releasing a turtle to the wild confers good karma.[10]

These nonavian reptiles are common in our culture, have been around a long time, and are diverse. We have discussed the general adaptations they have to allow for life on land. Beyond that, the crocodylians, lizards, snakes, and turtles are quite different from one another. Now, let us consider each group separately and look at a few of the impressive predators among them.

WHAT IS A CROCODYLIAN?

Recognizing a crocodylian does not require an academic degree. They all have elongated bodies extending into a thick, laterally compressed tail, and four short but robust limbs. There is a large,

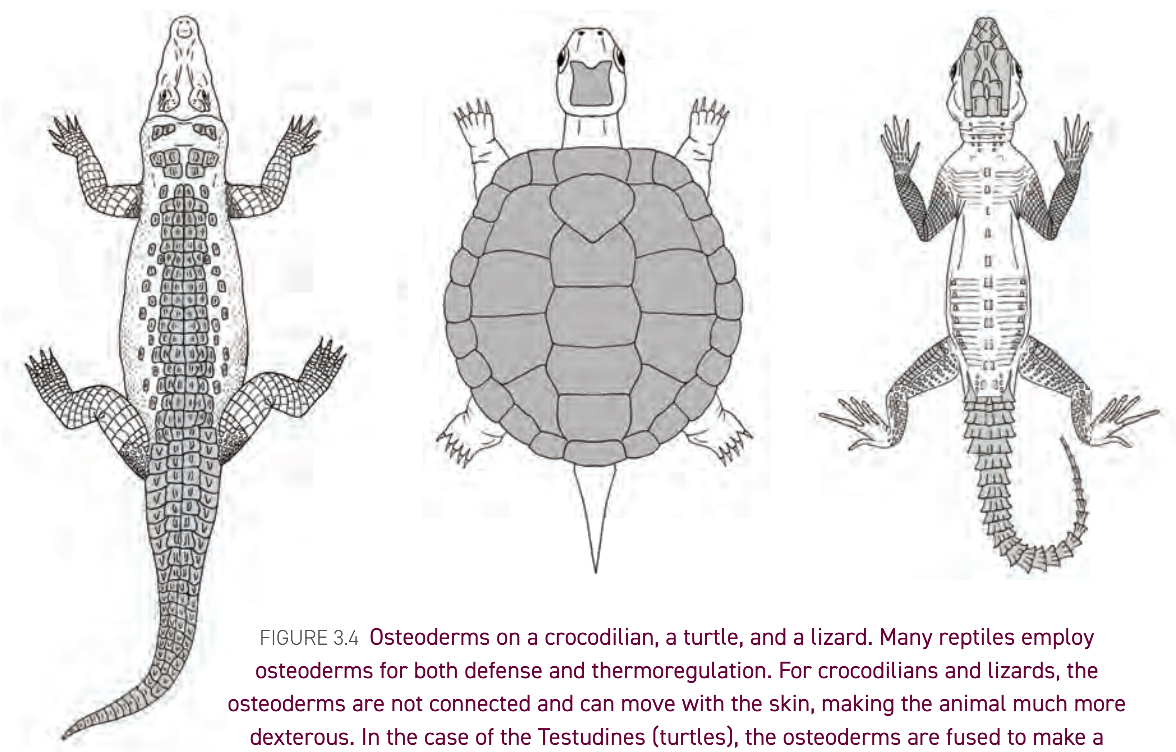


FIGURE 3.4 Osteoderms on a crocodilian, a turtle, and a lizard. Many reptiles employ osteoderms for both defense and thermoregulation. For crocodilians and lizards, the osteoderms are not connected and can move with the skin, making the animal much more dexterous. In the case of the Testudines (turtles), the osteoderms are fused to make a solid outer shell, trading mobility for being able to take your house with you.

heavy skull with a long snout and a jaw filled with teeth. They have scales, but underneath are thick, bony plates called *osteoderms* (bony skin) (fig. 3.4), armoring the body. Not much can take a bite out of an adult crocodylian (except Jaguars; see chapter 5).

There are about 27 species of crocodylians, divided among three groups: the Crocodylidae, Alligatoridae, and Gavialidae (fig. 3.5).[11] Most live in tropical climates, but the American and Chinese Alligators (*Alligator mississippiensis* and *sinensis*), American Crocodile (*Crocodylus acutus*), and Yacare Caiman (*Caiman yacare*) have ranges extending into temperate zones. As we noted above, there are some large ones, but forest-dwelling species less than 6 ft (2 m) long inhabit Africa and South America. The alligators and caimans are all associated with fresh water and are limited to North and South America, except for the Chinese Alligator. Crocodile species inhabit both fresh and salt water, so they are more widely dispersed than alligators. Saltwater Crocodiles are found in the Indo-Pacific and from the Indo-Australian archipelago into Australia. The Nile Crocodile inhabits the Nile River basin and freshwater marshes and estuaries throughout sub-Saharan Africa and Madagascar. The Mugger Crocodile (*Crocodylus palustris*; the Hindi word for "crocodile" is *maggar mach*) prefers fresh water, including irrigation ditches and backyard ponds, throughout India and Pakistan. The American

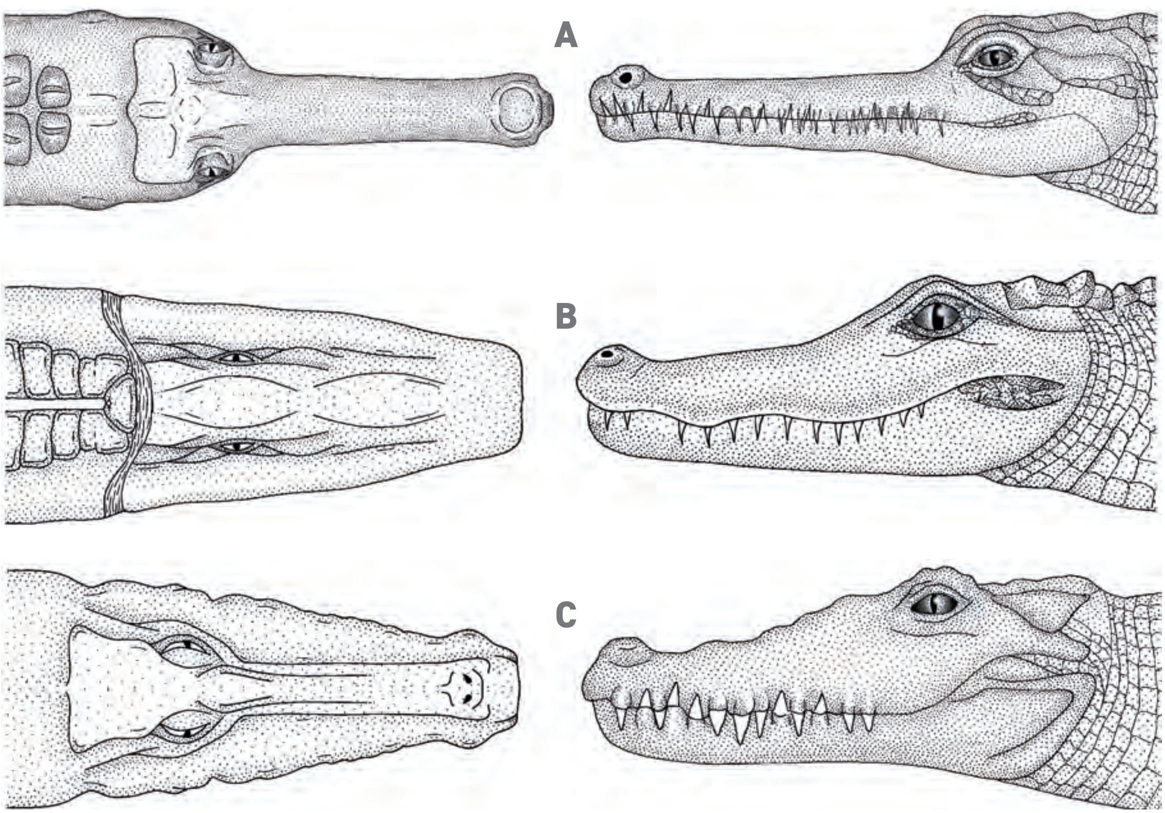


FIGURE 3.5 Comparison of crocodylian head morphology. (A) Gharial, (B) Crocodile, (C) Alligator. Note the difference in skull structures. The thin snout of the Gharial is more specialized for fish, which makes it more dependent on a single food source.

Crocodile is found along coasts from southern Florida through the Caribbean, and into northern South America.

The gavials include just two species: the Gharial (*Gavialis gangeticus*) and the False Gharial (*Tomistoma schlegelii*). The former is restricted to a small area of the Ganges River. The latter is found in the Malay Peninsula, Sumatra, Borneo, and Java. Both are characterized by their very slender snout in comparison with the other two groups (fig. 3.6).

BIOLOGY AND ECOLOGY

Crocodylians all spend most of their time in the water but, as ectotherms, come ashore to bask in the sun and heat up on cooler days. Alligators are the most tolerant of cold temperatures, and American Alligators can sometimes be seen in the winter hunkered down in the mud with their nose poking up through the ice. Chinese Alligators hibernate during winter. The most aquatic of the crocodylians are the gavials, which are characterized by their front teeth, both top and bottom, protruding outside their closed mouth in their narrow, fragile-looking snout (fig. 3.6).

As we noted, gavials are easily identified by their weird snouts. You can also distinguish alligators and caimans from crocodiles by their snouts (fig. 3.5). Alligators and caimans have a rounded snout, whereas crocodiles all have a narrower snout with a big fourth tooth on the lower jaw visible on both sides when the mouth is closed. Distinguishing that visible fourth tooth requires a rather close look, though. Fortunately, at least for identification purposes, there are not many places in the world where you still find both varieties in nature.

Before you go looking too closely at a crocodile's teeth arrangement, consider that although they are proficient swimmers, with a smooth, lateral motion of the tail propelling them forward while the back feet steer, they are also quite good at moving on land. They can do a *belly crawl* and *belly run* where the legs remain splayed out to the side such that

FIGURE 3.6 False Gharials (*Tomistoma schlegelii*) in Thailand. The Tomistoma (or False Gharial) is a specialized fish hunter, and its snout is adapted for that. Note the protruding teeth of both jaws, characteristic of the gavials.

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