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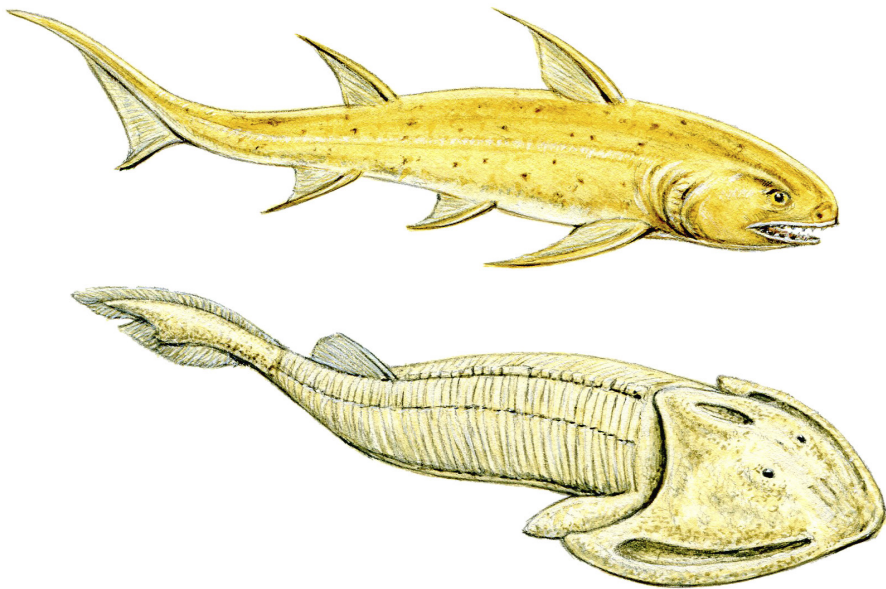
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eventually gave rise to plantlike cyanobacteria, which were able to photosynthesize and, therefore, to generate the oxygen in our atmosphere. In due course, life advanced to be multicellular and became more complex. Then animals appeared: sponges arose, followed by worms, jellyfish, and eventually early fish around 530 MYA.

Despite their modern-day counterparts coming in many different shapes and sizes, all sharks and their relatives actually derived from one single common ancestor. The lineage that gave rise to our contemporary sharks first appeared some 450 MYA or so. At this point, the cartilaginous fishes, including the sharks, skates, rays, and chimaeras (if you remember, these are known collectively as chondrichthyans) branched away from the bony fishes (osteichthyans).

A commonly cited figure is that the first sharks arose 440 MYA. To some extent this is true, as the earliest examples of sharklike dermal denticles can be dated to that time, but this assertion is a little misleading. It might be a stretch



ACANTHODIAN AND JAWLESS FISH

A typical acanthodian (top) compared to a jawless fish of the time.

to say that fish living during this period were genuine sharks, since the question of which sharklike creature had enough of the required characteristics to make the claim that it was undeniably the earliest shark remains unanswered.

What is not unresolved is an event that occurred during the end of the Ordovician Period, no later than 450 MYA: the evolution of jaws. Jaws were a game-changer, shifting the path of vertebrate evolution forever. The two earliest groups of jawed fishes, placoderms and acanthodians, were no longer limited to vacuuming up their dinner from the ocean floor like their jawless ancestors; they were now able to bite, chew, and crush their food, and manipulate prey in their mouths. The presence of jaws changed their entire approach to life and expanded their habitats, opening up a wide range of different niches which could now be explored and exploited. This led to an explosion of new species that defined the Age of Fishes. In fact, every major clade (taxonomic group) of fishes—sharks included—that we know and love today arose during this magical time.

THE ONE AND ONLY

It is difficult to say with any certainty when exactly the first shark appeared for several reasons. First, after death, cartilaginous skeletons of chondrichthyan fish degrade quickly and only heavily mineralized parts like the vertebrae fossilize. This means only patchy examples of ancient sharks exist in the fossil record. Complete shark skeletons are very rarely discovered, leaving paleontologists to rely almost solely on teeth and skin scales, which also fossilize relatively well thanks to their hardened coatings.

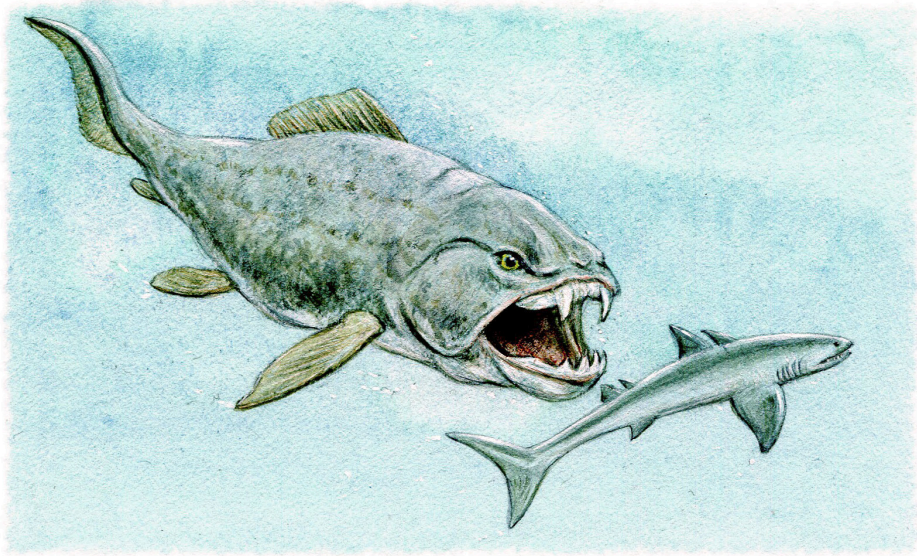
What's more, it is difficult to categorize early shark ancestors because evolution is mostly a gradual process, with subtle adaptations slowly shifting into larger changes over many millions of years. In more derived species (those that arose later on the evolutionary tree), it is easy to tell a chondrichthyan from an osteichthyan because skeletons of the former are made

up entirely of hardened cartilage, which never ossifies into bone. However, during the early stages, when these branches first separated, there were many crossovers and shared features between the groups, which were challenging to untangle.

One such group was the acanthodians, which were prematurely dubbed the “spiny sharks,” thanks to their sharklike shape and multiple pairs of fin spines. Their resemblance to sharks—with streamlined bodies, skeletons made of cartilage, and functional jaws filled with sharp teeth—masked the fact that acanthodians were actually a mosaic of both chondrichthyan and osteichthyan traits. No other shark, past or present, possesses multiple pairs of spined fins. However, two recent scientific papers concluded that acanthodians are indeed the true stem chondrichthyans. The other group, which at one time was thought to have given rise to sharks (and bony fishes as well), was the placoderms, a highly successful assemblage of dominant predators with a bony endoskeleton and a hinged, ossified, helmeted head. Placoderms, however, exhibited some anatomical dissimilarities to chondrichthyans and bony fishes that disqualified them from being considered ancestral to both groups.

After the rise of the acanthodians during the Ordovician Period (485–444 MYA), the fossil record reveals that there were many different species with sharklike forms, but it is hard to state with absolute certainty which—if any—was actually the first true shark. Most notably, it is difficult to determine whether some of the iconic early sharklike creatures were really sharks or part of a closely related sister-group, the chimaeras. Rather ominously dubbed ghost sharks, rat fish, or spook fish, but formally known as holocephalans, chimaeras branched away from the rest of the chondrichthyan fishes around 421 MYA, but there were many species along the way which were a bit like sharks and also a little like chimaeras.

We may never be able to unequivocally state which was the first true shark, and it is probably more realistic to identify a collective or a continuum of species which eventually evolved into sharks as we now know them. Scientists refer to these animals as stem chondrichthyans because they were neither true sharks nor genuine chimaeras, but have some features of each.



EARLY SHARK EVADING *DUNKLEOSTEUS*

During the Devonian Period, nimble sharks known as Cladoseleache were adapted to evade heavy, armored predators called Dunkleosteus.

One of the oldest sharklike stem chondrichthyans is the appropriately named *Doliodus problematicus*, which lived some 400 MYA. These creatures were a problematic mish-mash, with a sharklike head (including teeth, braincase, and jaws), but the body of an acanthodian (with several pairs of fin spines). Paleontologists suspect this creature might be the missing link between the ancient acanthodians and sharks proper.

Slightly later—around 390 MYA during the Devonian Period—a group known as the cladodont sharks arose. Within this group, members of the genus *Cladoseleache* are commonly referred to as the first real sharks, but others argue they were actually more likely chimaeras. This group of creatures was unusual because their skin was thin and relatively fragile compared to the hardened scales which make other sharks' skin so tough. But this was not a weakness! On the contrary, it allowed *Cladoseleache* to be nimble and quick. At the time, the mighty, armored placoderm fish known as *Dunkleosteus* roamed the oceans and the light frames of *Cladoseleache* probably allowed them to evade these larger, heavier predators.

A GOLDEN AGE

While the process of evolution is awe-inspiring, it can also be incredibly violent, continuously weeding out those too weak to survive. Even those organisms that pass the test of survival of the fittest often fall prey to massive extinction events periodically devastating the planet's biota. Near the end of the Devonian Period, a cascade of several mass extinction events over some 500,000 to 25 million years changed the Earth forever.

Whether this parade of catastrophes was caused by a destructive meteor, a major crash in ocean oxygen levels, sea level shifts, climate change, or some fiery supervolcano, we may never know for certain, but we do know that the marine world was devastated. During the End-Devonian Extinction (also called the Kellwasser Event) 371–359 MYA, about 70 percent of all marine life went extinct. Reefs almost completely disappeared and whole groups of trilobites (extinct marine arthropods), shellfish known as brachiopods, and the placoderms were completely wiped out. But all this death actually made way for the sharks to rise.

Sharks rule

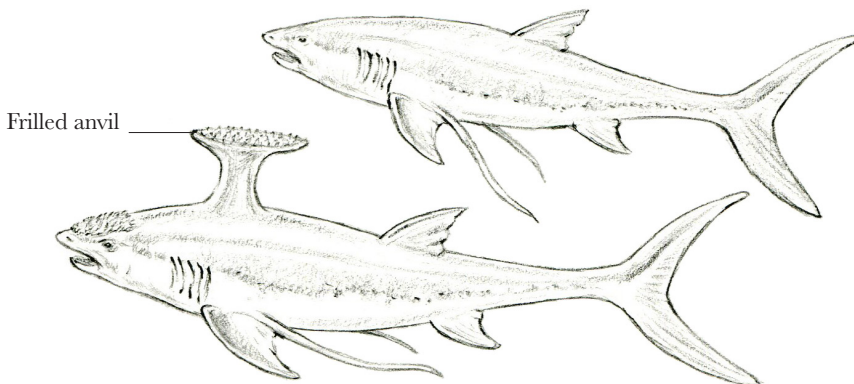
What followed was the Carboniferous Period (some 359–299 MYA). At this time, tectonic drift had formed two major oceans, where warm, shallow waters often flooded over the new supercontinent, Pangaea. The climate was continuously hot and humid, with indistinct seasons. On land, vast bogs and dense swamp forests stretched across Pangaea, while high atmospheric oxygen levels fueled unparalleled growth of insects to gargantuan sizes—millipedes the length of cars and dragonflies with wings measuring 3.3 ft (1 m) across. In the oceans, sharks ruled.

Bony fishes and the early sharks had not only survived, they had thrived! With the extinction of many of the primitive jawless fishes and the armored placoderms, sharks and their relatives were freed from a huge competitive burden and had more space to flourish. Amid recovering reefs hosting starfish,

urchins, marine worms, and sea snails, chondrichthyan fishes exploded into a multitude of different (often fantastically bizarre) forms and ecological niches. In fact, this period is known as the Golden Age of Sharks.

At the beginning of this period, some 340 MYA, there lived a group of fishes of the genus *Saivodus*. Reaching incredible sizes, up to 26 ft (8 m) from snout to tail, and boasting the classic streamlined, multi-finned shape so recognizable as shark-like today, these creatures can undeniably claim to be sharks (maybe even *the* first true sharks). Yet, later in the Carboniferous, there was also a multitude of other fantastical sharklike animals that may have been true sharks or perhaps more accurately chimaeras. One such group was the genus *Stethacanthus*. Arising around 330 MYA, male stethacanthids boasted a truly fantastical, frilled anvil resembling a wire scrub brush that stuck straight out from the top of their heads. This adapted dorsal fin, which scientists muse may have been inflatable so it could become engorged during courtship displays, is thought to have been a sexual ornament that arose to attract females. No modern sharks possess anything like this.

Similarly, a little later on in the Carboniferous (some 320 MYA), male *Falcatus* sported a unicorn-like, elongated first dorsal spine that stuck out from the front of their face. Like the anvil of *Stethacanthus*, the spines of *Falcatus* were



SEXUAL DIMORPHISM OF *STETHACANTHUS*
The frilled anvil of the male Stethacanthus (lower)
likely evolved to attract a female for mating

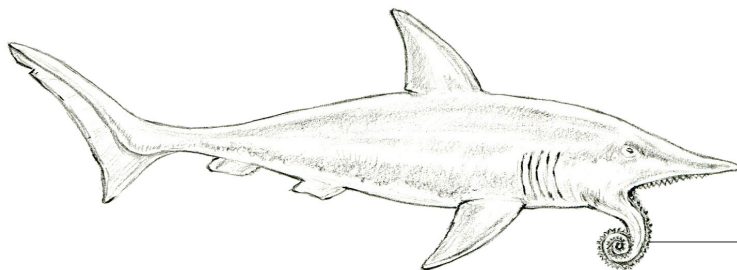
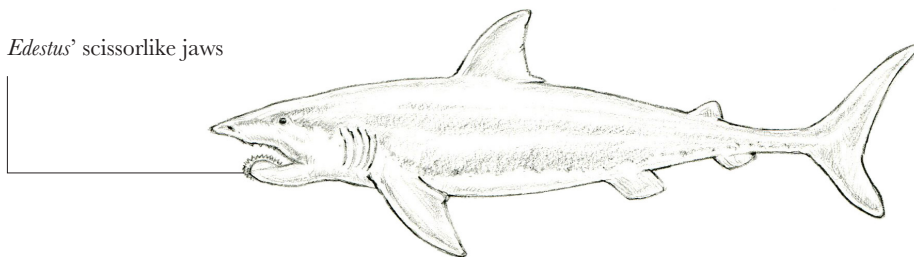
sexually dimorphic (different in males and females). Scientists think the spines evolved as a display of strength that *Falcatus* used to attract a mate and over time sexual selection favored larger spines, causing the appendage to become ever-more pronounced.

Give it a whorl

Around 299 MYA, the oxygen-rich Carboniferous gave way to the Permian Period. After a massive decline in atmospheric carbon dioxide led to pronounced climate change, drying, and major glaciation, rainforest ecosystems collapsed across the supercontinent and life on land changed forever. In the single super-ocean that spanned the entire globe, encircling Pangaea, waters teemed with snails, spiral-shelled mollusks known as ammonoids, and graceful, wafting feather stars called crinoids.

It is probably during this period that the most iconic of the sharklike ancestors lived (although it may more accurately be described as a chimaera): the magnifi-

Edestus' scissorlike jaws



Helicoprion's
helical jaws

JAWS OF PERMIAN SHARKS

*During the Permian Period, the extinct sharklike fishes
Helicoprion and Edestus had crazy jaw morphologies.*

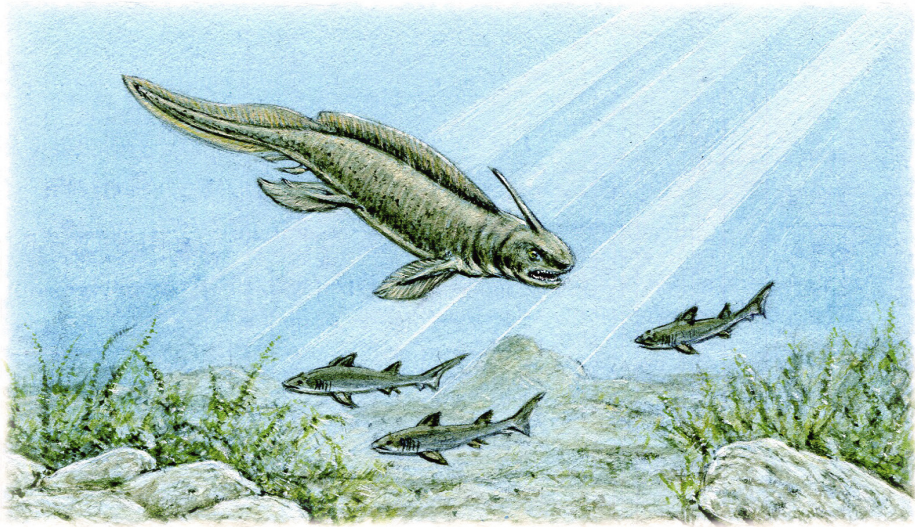
cent group in the genus *Helicoprion*. Arising around 290 MYA, these bizarre fishes sported a remarkable whorled jaw that projected as a tooth-lined spiral from the front of their face. This feature, which gave the shark a unique, chopping bite, arose because these animals never lost any of their teeth, as modern sharks do. Yet new ones didn't stop growing either. This resulted in the newly growing teeth at the back of the jaw pushing the older teeth out to the front, forming a wonderfully weird helix. This so baffled paleontologists when they first discovered it that they wondered if it was some heretofore undiscovered ammonite.

During this time there also existed a group of close relatives, known as *Edestus*, or more commonly the Scissor-toothed Shark. These creatures also never lost teeth, but in their case, this caused the jaw to extend and project forward and outward. Scientists think this made *Edestus* perfectly adapted to hunting because, unlike any other known shark, the remarkable scissor-mouth meant they could move their body up and down to slash prey with staggering force.

A NEW HOPE

Around 252 MYA, unimaginable volcanic eruptions caused catastrophic global warming and massive changes to ocean chemistry, which resulted in the largest extinction event to date. During what has become known as The Great Dying (also referred to as the Permo-Triassic Extinction Event, or the End-Permian Extinction), as many as 81–96 percent of all marine species, including corals and trilobites, were completely wiped out and 70 percent of all land animals were also killed off. This marked the end of the remarkable diversity enjoyed during the Golden Age of Sharks.

Edestus and the cladodont sharks did not make it, yet several early shark lineages did survive this catastrophic extinction event. Experts suspect that they retreated into deep-sea, offshore refuge areas to ride out the changes going on around them. It is during this period (about 200 MYA) that we start to see evidence of the first



XENACANTHS AND HYBODONTS IN RIVER ECOSYSTEMS
Ancient sharks thrived in freshwater river ecosystems during the Triassic Period.

modern sharks, known as neoselachians, in the fossil record. Alongside them, their sister groups, the hybodont sharks and the xenacanthiforms, also survived into the new post-extinction period, flourishing in the brackish (somewhat salty) and freshwater environments of rivers, as well as in the oceans.

Hybodonts had the familiar sharklike form, yet they were incredibly diverse, especially in their teeth, so much so that many dental fossils from this time remain unidentified or unnamed. Hybodonts were the dominant group during the Triassic and into the Early Jurassic Period (240–230 MYA). However, the hybodonts eventually began to be overtaken by the neoselachians toward the end of the Jurassic.

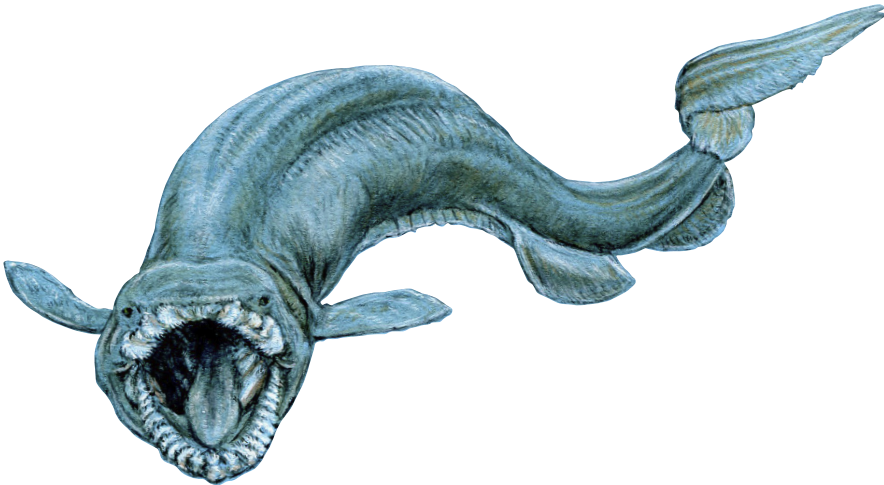
Sadly, the end of the Triassic (around 228–201 MYA) saw another global extinction event called the Triassic–Jurassic Extinction. A gradual change in climatic conditions, changing sea levels, and ocean acidification over approximately a 30-million-year period yet again caused the extinction of up to 75 percent of all marine and terrestrial animals.

Jurassic shark

But with every end there is a new beginning and after this tragedy, we see the rise of some of the most iconic animals in the history of our Earth: the dinosaurs. Is there anyone on our planet who doesn't know about this period in geohistory? Even its name—the Jurassic Period (201–145 MYA)—is familiar thanks to the blockbuster movie franchise. Yet many people don't realize that this era boasted not only gigantic lizards, but also magnificent sharks.

While many shark lineages were once again wiped out in the preceding mass extinction, some persisted and enjoyed quite a long period of relative stability afterward. Sharks subsequently became very common in the oceans, and they began to diversify readily and rapidly into some of the forms familiar to us today. In fact, the majority of modern sharks and rays originated during the Early Jurassic Period, with at least five of today's nine major groups (taxonomically known as orders) all arising during this time.

For example, around 195 MYA, the first hexanchid sharks appeared. This lineage gave rise to the modern hexanchiform sharks, including the six-gills and seven-gills that are still swimming in our oceans today. In fact, some of the



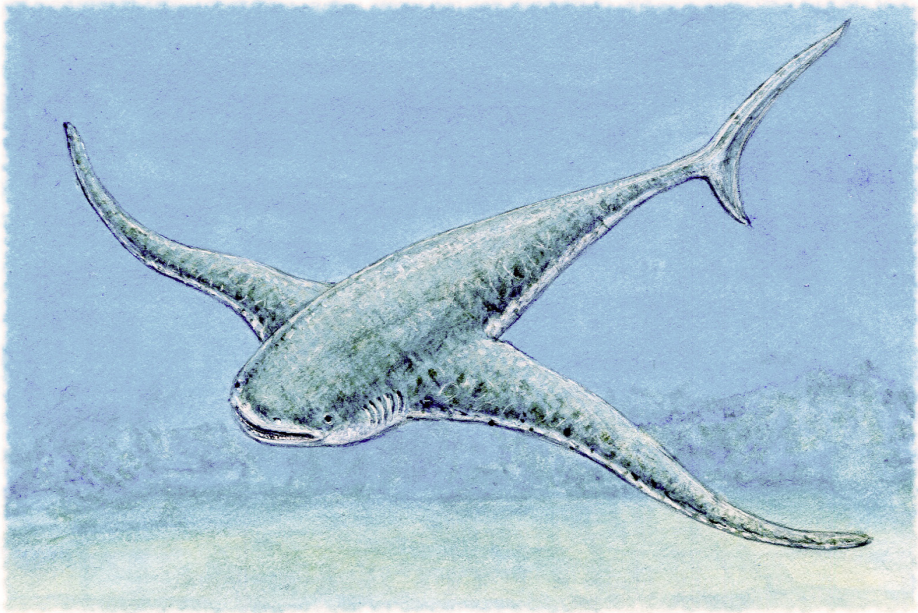
FRILLED SHARK

Frilled Sharks are known as “living fossils,” as they have been swimming in the oceans since the time of the dinosaurs.

species in this group, such as the Frilled Shark (*Chlamydoselachus anguineus*), have been around for so long that they are known as “living fossils” and have remained basically unchanged for millions of years.

Around 168 MYA, the first catsharks appeared, ancestors of today’s Small-spotted Catshark (*Scyliorhinus canicula*) and their relatives. At a similar time, early White Shark (*Carcharodon carcharias*) ancestors known as *Paleocarcharias* also came into being. The earliest ancestors of the Spiny Dogfish (*Squalus acanthias*) first appeared some 125 MYA. Then the first mackerel sharks (order Lamniformes) and stingrays appeared, some 135–130 MYA.

During this period, sharks developed more flexible, protruding jaws, which meant they could handle larger prey, even animals bigger than themselves. The speed with which they could swim also increased and, by 100 MYA, the so-familiar, large-bodied, speedy, modern sharks had come into being.



THE EAGLE SHARK

Aquilolamna evolved a soaring style of locomotion millions of years before the batoids developed the same swimming adaptation.

It was around 185 MYA that the earliest types of rays, known as *Protospinax*, first appeared. Scientists recently made an extraordinary discovery regarding the evolution of early rays, after finding a fossil of a new species of shark called *Aquilolamna* (*Aquilolamna milarcae*). Living alongside the dinosaurs around 93 MYA, the aptly named Eagle Shark had a broad mouth (similar to many rays), which scientists think was used for filter-feeding. It had a large tail fin (much like a modern shark), which it used to swim, but also sported elongated, winglike pectoral fins, spanning a whopping 6.3 ft (1.9 m) across. Thus, it would seem that these sharks “flew” through the water, using their fins for propulsion and maneuverability, much like modern-day manta rays.

This finding is remarkable because it changes everything we thought we knew about when this mode of swimming first appeared and how this adaptation arose. *Aquilolamna* proves that soaring arose as many as 30 million years before the ancestors of today’s manta and devil rays (family Mobulidae) popped up with the same body plan. As this shark is thought to be more closely related to modern Lamniformes (early relatives of the White Shark) as opposed to rays, this means that “wings” for underwater flight did not evolve just once but multiple times over the course of evolutionary history.

Scientists suspect that *Aquilolamna* was wiped out by the K-T Extinction Event (aka the Cretaceous–Tertiary Extinction) that occurred 66 MYA. While you might not have heard the name, this extinction event is familiar to us all because it signaled the end of the dinosaurs and heralded the ascendancy of mammals. When a mighty asteroid struck the Earth, creating an impact crater over 90 miles (150 km) wide, enormous amounts of dust and ash were flung into the atmosphere, causing an immediate global climate shift. This killed 75 percent of all species, including many plants, all ammonites, mosasaurs (a group of extinct aquatic reptiles), and, of course, the dinosaurs. In the oceans the vast majority of very large predatory sharks and huge numbers of rays were driven to extinction, with about 85 percent of all species dying out. The diversity of larger-bodied members of the order Lamniformes was especially reduced.

Off the scale

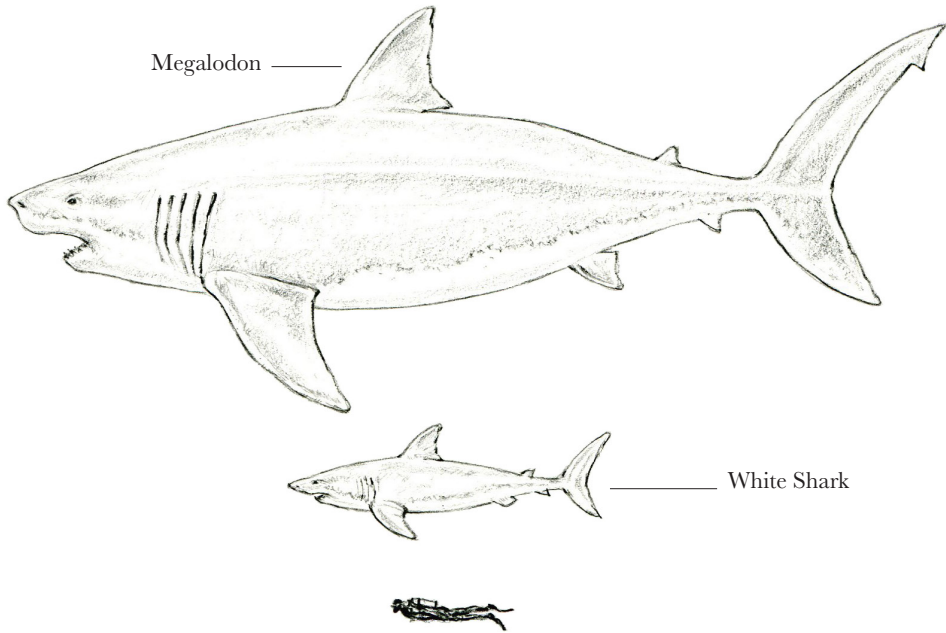
This brings the total of mass extinctions that the sharks have managed to survive to no less than four. What's more, recent scientific research has shown that another catastrophic event may have specifically affected sharks. After developing a new method for analyzing fragments of teeth and fossilized skin scales known as ichthyoliths within seafloor sediments, scientists have discovered a heretofore unknown shark extinction that happened as recently as 19 MYA. We now know that during the Miocene Epoch (23–5 MYA), shark abundance dropped by as much as 90 percent and there was a 70 percent reduction in shark diversity across many different lineages all around the globe. Especially impacted were pelagic species of sharks—those that live in offshore habitats, far from land.

It seems that these families never fully recovered from such catastrophic declines. While the modern shark lineages began to resurge some 2–5 million years after this mass extinction, the loss of so many different species of sharks completely shifted the makeup of shark communities and this has reverberated through evolutionary lineages all the way through to the present day. As a result, our modern sharks, as fascinating and diverse as they are, may actually represent only a tiny fragment of what they once were.

The Meg

We couldn't possibly write a biography of sharks, telling the story about ancient shark ancestors, without devoting some time to the magnificent, mighty *Megalodon*, a beast which lived from 23 to about 3.2 MYA. Known to scientists as *Otodus megalodon*, the name literally means “mighty teeth.” *Megalodon* was the largest macropredatory shark that ever lived. In fact, it was *the* largest predatory fish that ever lived. A single tooth alone could reach 7 in (18 cm) in length and their jaws could open wide enough to engulf the front of the average car!

As with other chondrichthyans, what we know about *Megalodon* has predominantly been learned by studying their fossilized teeth. Through a method known as allometry, scientists can look at the ratios of body parts of shark species that are alive today and use this to calculate how big an extinct shark would have been, based only on measurements from a tooth. However, as this



MEGALODON COMPARED TO THE WHITE SHARK

The extinct Megalodon could reach sizes of 60 ft (18 m) in total length, dwarfing even the largest modern-day White Sharks.

is not an exact science, we are not completely certain how large a size the Meg could achieve. As the most recently accepted length is about 60 ft (18 m), Megalodon was truly gargantuan. Imagine a shark the length of a semitrailer swimming past you (but not toward you) in the water.

Megalodon evolved to become so much larger than its ancestors, thanks to a size-based arms race between predator and prey. Over millions of years, as prey evolved to be larger and thus more difficult to hunt, predators evolved to become bigger ... prey then became larger still ... and so on. This vicious cycle pumped body forms to enormous sizes over the span of millions of years, culminating in the incredible Megalodon. This gigantism may, in fact, have contributed to Megalodon's downfall. Toward the end of the Meg's reign, an ancient climate change event caused significant global cooling. As this meant a lot of the ocean was now too cold for them, this once global, cosmopolitan predator's habitats constricted hugely and many of their favorite prey shifted

their distributions as well. Concurrently, large predatory whales and the White Shark arose, and began competing with Megalodons for any of the food supplies that remained. Their wider thermal tolerance and more modest caloric requirements (thanks to their smaller size) meant that White Sharks were able to outcompete the Megalodon for prey, so eventually, they prevailed, and their lineage persisted, whereas Megalodon was driven to extinction.

Having arisen from a previous ancestor known as *Otodus obliquus* some 23 MYA, Megalodon was a part of the order Lamniformes, which today includes White Sharks, Basking Sharks, and Sand Tigers (more on this in chapter 3). At one point, scientists thought the Meg's closet next of kin was the White Shark, but we now know that this is not the case. In fact, studies of tooth morphology have elucidated that Megalodon was actually more closely related to modern-day Makos. This makes the Shortfin and Longfin Makos (*Isurus oxyrinchus* and *I. paucus*, respectively) Megalodon's closest living relatives and means Megalodon is not the ancestor of our contemporary White Sharks, as their lineages actually diverged around 100 MYA.

A question that shark scientists often get asked is, "Are Megalodons definitely extinct?" and the answer, unequivocally and without any uncertainty is "Yes"; Megalodons are definitely gone. Rigorous statistical analysis of the dating of Megalodon fossils tell us that they had died out no later than about 3.2 MYA. There have been no samples of Meg teeth or any other body part, fossilized or fresh, found anywhere in the world that are younger than this. If Megalodon was still around, we would certainly expect to find something, considering how prevalent they were in the fossil record in previous periods. What's more, we also never see any evidence that a gigantic macropredatory shark is living somewhere in our oceans, unseen; no huge bites on whales or other potential prey and no observations of the beast itself. All "sightings" of Megalodons have in fact been proven to be other species, like White Sharks, mako sharks (*Isurus* species), and often Basking Sharks (*Cetorhinus maximus*), which actually look nothing like the Meg. While it is true that our oceans are massive and largely unexplored, this does not mean Megalodons could still be out there. There is simply too little food in the deep-sea, offshore environments to support

such an enormous predatory animal and they would not be able to survive the cold of the abyssal regions, like the Mariana Trench. Don't believe all the conspiracy theories you find on the internet or put too much stock in monster movies that are designed only to entertain, not inform; there is no doubt at all that Megalodon is, perhaps sadly, as dead as the dodo.

IT'S NOT OVER

Many people think of evolution as something that happened in the deep past, but on the contrary, it is a never-ending process. Both extinct ancient sharks and their extant counterparts are part of a continuous story of adaptation, disaster, change, and survival against all the odds. For example, the order Carcharhiniformes, to which Sandbar Sharks (*Carcharhinus plumbeus*) belong, first appeared in the Jurassic Period and modern mako sharks have been around for only some 60 million years. Although this might sound like a long time ago, it means these sharks and many others alive today are relatively new kids on the block compared to the chondrichthyan lineage as a whole. And ongoing environmental shifts, genetic mutations, and selection pressures continue to drive changes in shark morphology, habitat, and behavior to this day, although some of these changes (morphology, for example) operate on longer time scales than others (such as habitat changes).

New and improved

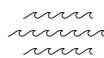
One example of evolution in sharks, a rather atypical one, is that of the Epaulette Sharks (*Hemiscyllium ocellatum*) in Australia, which have evolved to “walk” short distances on land. When the tide recedes, and small tide pools become isolated by stretches of sand and coral heads, these little sharks use their strong fins to move between submerged areas. Not only has their fin morphology allowed for this bizarre enhancement, but they have also evolved a remarkable hypoxia tolerance to do this—they are able to survive in very low oxygen.

While they are exposed to the air and unable to ventilate, Epaulette Sharks can widen their blood vessels to lower their blood pressure, which ensures oxygenated blood continues to reach the most important organs like the brain and heart. They have effectively evolved to be unparalleled breath-holders. Take as another example the hammerheads (family Sphyrnidae). This is one of the newest shark families, evolutionarily speaking, having arisen a mere 35 MYA. These sharks are absolutely iconic, boasting an otherworldly, elongated and flattened, mallet-shaped face known as a cephalofoil. These fantastical features may be cool to look at, but they also confer some adaptive advantage to the sharks which enhances their ability to survive—a remarkable feat of evolution. As the appendage is formed by the lateral expansion of cartilage housing the sensory regions, the cephalofoil provides the hammerheads with a marked advantage in sensory perception. Compared to other sharks, the elongated distance across their face gives them an enhanced sense of smell, better electro-sensory perception, an enlarged visual field, and excellent binocular vision.

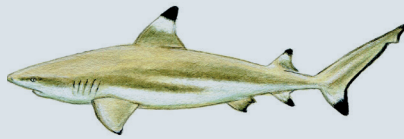
All these super senses mean that hammerheads are superbly evolved for their lifestyle. As if that wasn't enough, the strange head can also be used to pin prey like batoids to the seafloor while the shark consumes them. It can act as a forward rudder facilitating sharp turns. However, this incredible specialization might doom these remarkable sharks eventually. Scientists are now concerned that hammerheads are so specialized that they have been backed into a corner, evolutionarily speaking, and in today's anthropogenically driven, changing world, they may not be able to continue to adapt fast enough to their shifting environment.

* * *

With sharks continuing to evolve subtly as you read this, some species will probably very sadly be driven to extinction, but who knows what sharks might look like and what they could be doing a hundred million years from now?



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3
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THE SHARK FAMILY TREE

WE ARE FAMILY

To construct a family tree, one must know the family members. So, we start this chapter on the shark family tree with a conundrum: shark taxonomists are unsure how many species of sharks even exist. In other words, they do not know all the family members. Today scientists have described no fewer than about 1,250 elasmobranch fishes (the sharks and batoids), but new species are being added every year. It is thus challenging to put a number on how many different types of sharks there really are.

In nature, a species consists of individuals that reproduce only with each other to produce viable and fertile offspring—that is, progeny that are basically healthy and capable of breeding when they mature. Each of the four sharks featured throughout this book is a distinct species. This means that, while a Great Dane is theoretically capable of reproducing with, say, a Chihuahua, since they are (perhaps incredibly) both in the same species (*Canis familiaris*), none of our shark species could do the same with each other.

You'd think it would be a relatively easy to work out the number of shark species, since distinct species don't look alike, right? That may be true for some organisms, but two different organisms can look identical and constitute different species. Consider the Carolina Hammerhead (*Sphyrna gilberti*), a sister species to the Scalloped Hammerhead (*S. lewini*), with whose range it overlaps along the coast of South Carolina in the southeast United States. The physical appearances of the cryptic species, the Carolina Hammerhead, and the established, named species, the Scalloped Hammerhead, are indistinguishable. The main anatomical difference between the two is that the Carolina Hammerhead has fewer vertebrae, but you'd need an X-ray machine or other imaging device to detect this. Yet, in 2006, a team of researchers from the University of South Carolina discovered that what shark biologists had always called Scalloped Hammerheads were actually two genetically different species.

How then do taxonomists discriminate between species? Recent developments in the application of modern molecular biology have led to discoveries

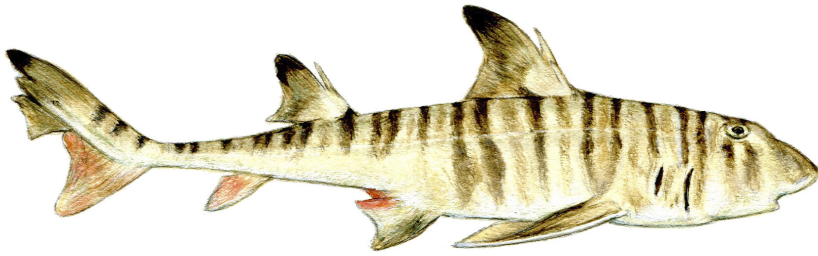
like the Carolina Hammerhead–Scalloped Hammerhead distinction, and these discoveries are occurring so quickly that it is making the heads of taxonomists spin as they attempt to confirm whether what molecular biology unearths in the lab also applies in nature.

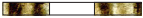
Another explanation for the uncertainty around the number of shark species is the lag in assessments of underexplored areas, most notably the deep sea, but also of remote locations in sparsely populated areas. Therefore, when a new species of shark is discovered, this doesn't mean it spontaneously arose right under our noses. Rather, it has existed for some time, but it has simply evaded detection by researchers.

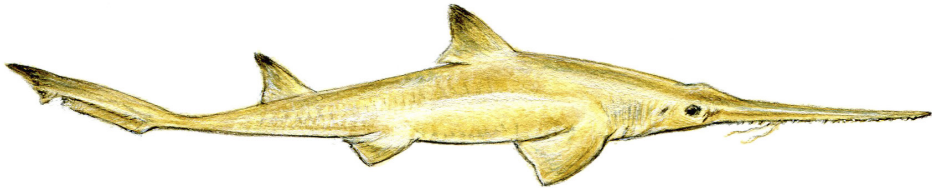
Where have you been all my life?

New species are discovered daily over a wide array of taxa across the spectrum of life, from amoebae to hedgehogs, so it isn't really surprising that new species of sharks are also being revealed. In the last ten years, around 54 new shark species have been identified, plus 100 batoids (rays and skates) and seven chimaeras. Some newly discovered sharks, besides the Carolina Hammerhead, include Lea's Angel Shark (*Squatina leae*), Halmahera Epaulette Shark (*Hemiscyllium halmahera*), Painted Hornshark (*Heterodontus marshallae*), Ridged-Egg Catshark (*Apristurus ovicorrugatus*), and two species of sawshark (not to be confused with sawfish, which are batoids), Kaja's Sixgill Sawshark (*Pliotrema kajae*), and Anna's Sixgill Sawshark (*P. annae*). Stunning beasts all, to be sure, but no large, legendary counterparts to the White Sharks (*Carcharodon carcharias*) or Tiger Sharks (*Galeocerdo cuvier*) have been added to the list recently.

What is the current best guess for the number of shark species? In 1984, the authoritative book on sharks, Leonard Compagno's *Sharks of the World*, listed 342 species of sharks. As we write, estimates from reliable and authoritative sources pin the number of taxonomically valid shark species at between 505 and 603, with batoids at 643–822 and chimaeras at 50–57, but by the time this book goes to press, it is likely that half a dozen new species will have been discovered and the numbers will already be out of date. As taxonomists validate these putative new species, we will continue to adjust our numbers.



3.5 in 
10 cm 



6 in 
17 cm 

RECENTLY DISCOVERED

The Painted Hornshark (top) and Kaja's Sixgill Sawshark, from NW Australia and Madagascar respectively, are two species only recently known to science.

You may be surprised to hear there are so many species of sharks, but is this actually a high number? For insight into that question, look no further than the bony fishes, whose number of species may exceed 35,000. Among these bony fishes, there are more members of the carp/minnow family (around 3,000 species) than all the sharks, batoids, and chimaeras combined. So, while yes, there is prodigious diversity of sharks in terms of size, shape, behaviors, adaptations, habitats, and so on ... no, their biodiversity actually pales in comparison to many other vertebrate groups. Biodiversity, however, is not the same as success (there is but a single living species of humans, although given the way we treat each other and the planet, maybe the word “success” doesn’t apply to us), and the success of sharks as a group, and their outsized ecological importance, cannot be denied.

The shark diaspora?

You are likely wondering why there are relatively few species of sharks. Species form in many ways, but one of the main modes involves separating part of the population from an existing species, after which the newly separated group may diverge from the original population and given enough time—*voilà!*—become a new species. The answer to why there are so few species of sharks plunges us to the depths of what it is to be a shark; that is, the shark's approach to life.

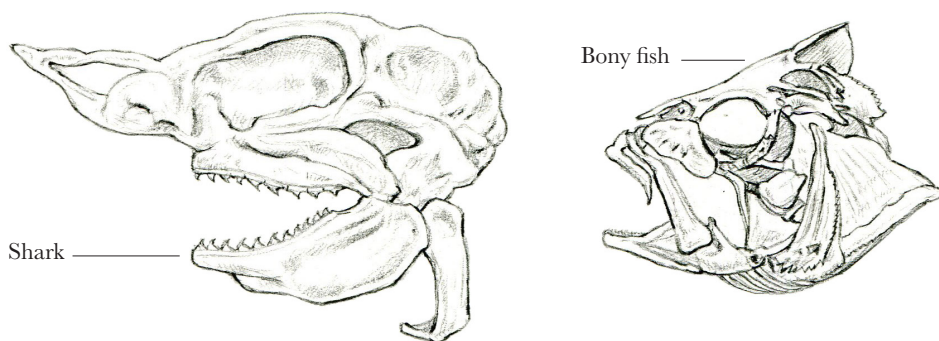
As a group, sharks and their close relatives have conservative life history characteristics, including slow growth, late maturation, long gestation periods, and relatively small numbers of young. All these features work against making new species. For instance, a key way for the separation of a population to occur is through mechanisms that facilitate dispersal. Bony fishes do a far better job of this than sharks. Some bony fish lay many millions of eggs, and they (or the subsequently hatched larvae) often become entrained in surface currents that disperse them—in some cases, all the way across ocean basins. Of course, most do not survive the voyage, but enough may do so to establish new populations, often in habitats very different from where they once lived, which given enough time may form new species. Sharks, on the other hand, have a few larger offspring that do not disperse like the bony fish. Most adult sharks are relatively small (less than 3.3 ft/1 m), so it would be risky to travel as far as bony fish eggs and larvae. Moreover, as many as 80 percent of shark species are benthic and have small home ranges as adults; they aren't dispersing either.

The diversity of bony fish species also ballooned due to the presence of an actual balloon, as bony fishes have an internal inflatable sac called a swim bladder, which they use to adjust their buoyancy. As a result, many bony fish species can hover almost wherever they choose in the water column. This adaptation allows them to occupy the abundant spaces in, say, coral reefs or mangrove systems. Sharks, which are heavier than water and must either rest on the sea-floor or swim continuously, simply cannot exploit these habitats similarly. The swim bladder also facilitated the evolution of a small size in bony fishes which, again, gave them an advantage over sharks in certain environments.

An additional explanation for the high diversity of bony fishes is the complex bone structure of their heads. Whereas the skull, jaws, and adjacent structures of a shark's head involves only a handful of parts (a skull, upper and lower jaw, and a few supporting cartilages), the bony fish head is a complex jigsaw puzzle of dozens of bones. This provided natural selection with the raw material to produce a bewildering array of head shapes and mouth variations, and thus a diversity of feeding styles and opportunities to exploit new prey sources. Through this process new species developed.

Think of it this way: a kid can remain occupied for weeks building innumerable, highly creative structures with several dozen Lego bricks, but boredom would quickly ensue if the child had only a handful. Yes, the bony fish head is the anatomical equivalent of a set of Legos!

The functional significance of head shape is that no sharks protrude from burrows to gobble plankton like jawfishes, pick individual planktonic shrimp from the water column like the Mandarin Fish, shoot a stream of water at insects resting on terrestrial vegetation like an archerfish, eat detritus like the Striped Mullet, pick parasites like cleaner wrasses, or scrape algae from coral reefs like parrotfish. For that matter, no sharks are herbivores.



SKELETAL STRUCTURE

Simple (shark) vs complex (bony fish), skeletal differences that have allowed bony fish to evolve more varieties of head shapes and feeding styles than sharks.

Finally, since only four species of sharks are known to penetrate rivers and lakes, for reasons that we explain in Chapter 4 (see page 93), freshwater ecosystems represent a lost opportunity for further speciation. That audible sigh of relief you may be hearing comes from the Largemouth Bass, Bluegills, and carp from your nearby streams and lakes. Life is tough enough for them without worrying about sharks as well.

Do Kings Play Chess On Fine Glass Sets?

Or perhaps you prefer Drunken Kangaroos Punch Children On Family Game Shows. Still confused? Both of these silly sentences—and numerous others that often start with “Did King Philip”—are mnemonic sequences for remembering the hierarchy of Linnaean classification, based on the first letters of the Domain-Kingdom-Phylum-Class-Order-Family-Genus-Species system.

So, let’s see where sharks are, taxonomically speaking, on the family tree we referred to earlier.

Domain Eukarya (Animals, plants, fungi, plus some single-celled organisms)

Kingdom Animalia (Organisms that do not photosynthesize or absorb their food)

Phylum Chordata (Animals with a skull and backbone, as well as around 3,000 kinds of oddball invertebrates like sea squirts that lack these)

At this point on the family tree, sharks share a branch with bony fish, other cartilaginous fishes, amphibians, reptiles, birds (or, more accurately, avian reptiles), and mammals (including you), as well as the jawless fishes and the extinct group of fishlike vertebrates known as placoderms that we mentioned in Chapter 2 (see page 42). To further distinguish sharks, we’ll need to add subdivisions to the system we just introduced. Sorry, but we are unaware of mnemonic devices to recall these.

Subphylum Vertebrata (Organisms with a prominent skull, vertebral column, and brain)

Superclass Gnathostomata (All of the above minus the jawless fishes: the hagfish and lampreys)

The classification so far does not distinguish sharks from other cartilaginous fishes, tuna, alligators, frogs, seagulls, your pet cat and dog, or even humans. That will be next:

Class Chondrichthyes (The “cartilaginous fishes,” including sharks, batoids, and chimaeras)

Subclass Elasmobranchii (The sharks and batoids)

If you recall, sharks and their cousins, the batoids (skates and rays) and chimaeras (ghost sharks), are all united as cartilaginous fishes in the class Chondrichthyes. All possess cartilage as their primary skeletal component, as well as the suite of other characteristics we introduced in Chapter 1 (see page 18). Within the Chondrichthyes are two subclasses: Holocephali (chimaeras, which mostly inhabit the deep sea) and Elasmobranchii, the most species-rich and diverse chondrichthyans. Elasmobranchs, as members of the subclass Elasmobranchii are commonly known, are further subdivided into three superorders:

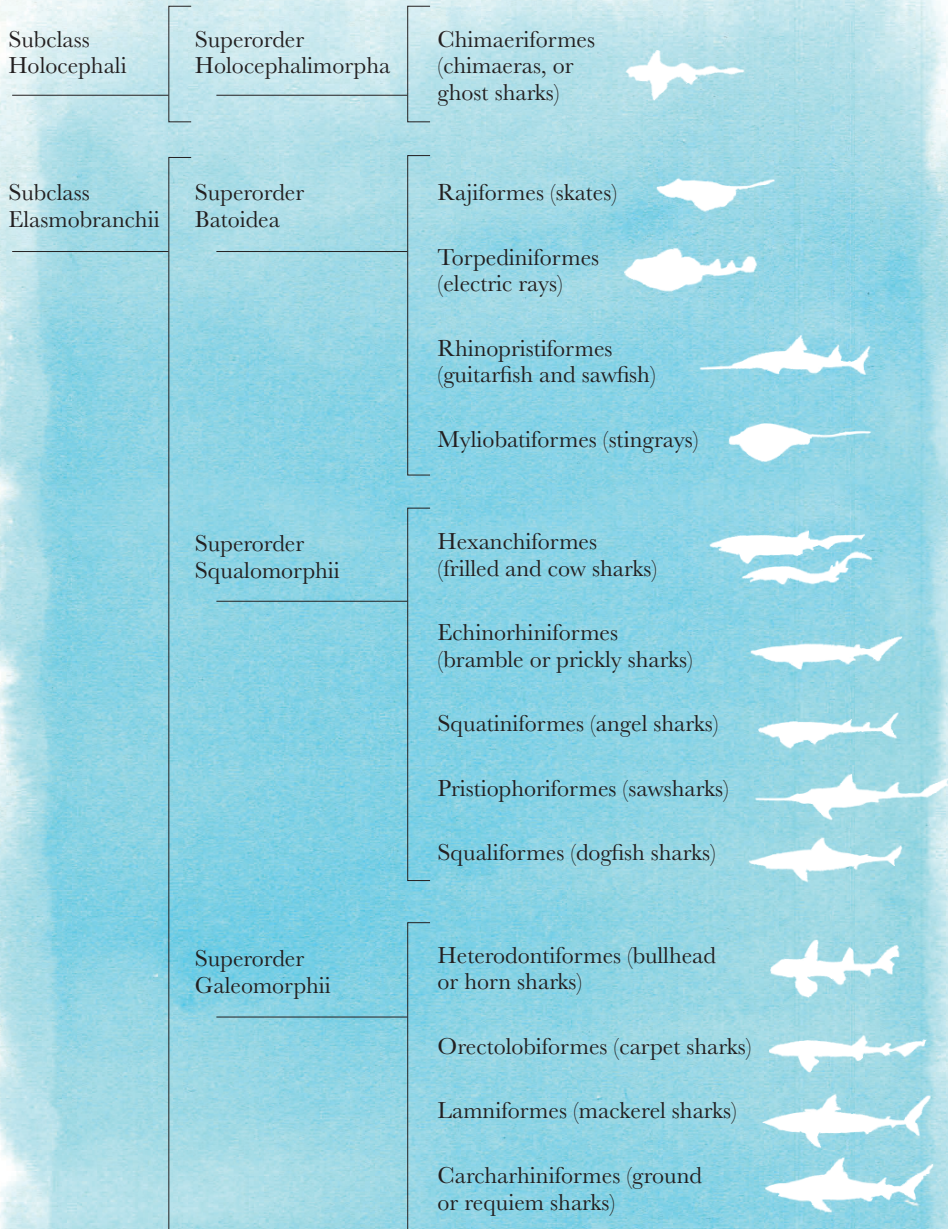
Superorder Batoidea (skates and rays; sometimes called Batomorpha)

Superorder Squalomorphii (dogfish sharks)

Superorder Galeomorphii (galea sharks)

Batoidea includes more than 650 species of skates and rays. The Squalomorphii includes some 183 mostly cold-water sharks and the Galeomorphii a diverse array of 367 or more species of sharks. Since there are more similarities uniting the elasmobranchs than differences separating them, this book could easily have been titled: *Elasmobranchs: The Illustrated Biography*.

To visualize how different species are related to each other and how they evolved through time, taxonomists plot them all on phylogenetic trees. These diagrams depict the lines of evolutionary descent of different species and divide creatures into increasingly smaller groups based upon similarities in morphology or genetics. This means that when you look at a phylogenetic tree, species positioned on arms nearer to each other are more closely related and probably have more similarities.



SHARKS AND THEIR CLOSEST RELATIVES

Sharks, skates, and rays are all united as elasmobranchs. Together with holocephalans (ghost sharks), they constitute the 1,250 or so species in the class Chondrichthyes.

YOU TWO COULD BE SISTERS

The batoids and both shark superorders are sister groups—that is, they are each other’s closest related group. As we learned in Chapter 2, the batoid lineage arose during the Late Triassic and Early Jurassic, between about 230 and 200 MYA, although some estimates go as far back as 266 MYA. Following the separation from the shark lineage, batoids evolved independently of sharks into the fascinating and diverse group that they are today. The superorder Batoidea comprises four orders: skates (order Rajiformes), electric rays (Torpediniformes), stingrays (Myliobatiformes), and guitarfishes and sawfishes (Rhinopristiformes).

The most easily discernible difference between sharks and batoids is their external form. The body plan of batoids consists of a flattened physique and the presence of “wings,” which are actually extended pectoral fins fused along the entire length of the body. Exceptions to this generalization include an apparently dissident group of batoids, the guitarfishes and sawfishes, which “decided” to remain somewhat sharklike in their body forms as well as their ecological role. Not to worry, the surefire way to distinguish that Smalltooth Sawfish (*Pristis pectinata*) or Shark Ray (*Rhinus ancylostoma*) from the Sandbar Shark (*Carcharhinus plumbeus*) or Spotted Catshark (*Scyliorhinus canicula*) swimming in your favorite aquarium is the placement of their gill slits: in every single batoid the pairs of gill slits are ventral (on the underside), whereas they are lateral (on the sides) in all sharks.

We now arrive in the weeds, so to speak, distinguishing the two shark superorders from each other. We could devote the rest of the chapter, even the remainder of the book, to this task, but we won’t. In the next few paragraphs, we’ll limit ourselves to what we consider salient summaries of a sampling of the distinguishing features of the major groups of sharks, including our four focus species.

Squalomorph sharks

Sharks in the superorder Squalomorphii (from *squal*, meaning “dogfish”) are a diverse group of about 183 species. These sharks are typically found in colder waters of mid- to high latitudes or in very deep water. To recognize each other

in the near pitch-black, many can glow in the dark. Squalomorph sharks are characterized by the loss of an anal fin in all but one group (the frilled and cow sharks) and having only moderate jaw mobility. They are the most primitive of the two shark superorders, having arisen between 279 and 190 MYA, and are organized into five orders:

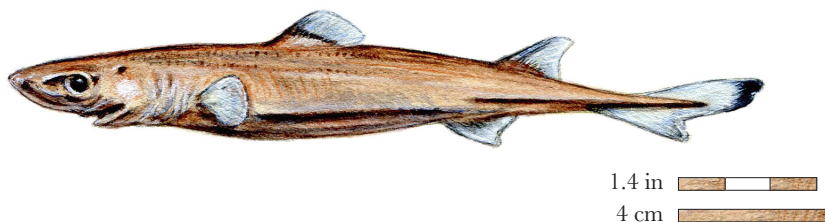
Hexanchiformes (frilled and cow sharks)

Echinorhiniformes (bramble or prickly sharks)

Pristiophoriformes (sawsharks)

Squaliformes (dogfish sharks)

Squatiniiformes (angel sharks)



TWO SPECIES OF SQUALOMORPH SHARK

Two species contesting for the title of most beautiful shark, the Rough Shark (top) and Dwarf Lanternshark (enlarged to showcase its magnificence).

Among the squalomorphs is the ancient lineage of Hexanchiformes, which all have more than five pairs of gill slits. This group includes the behemoth Bluntnose Sixgill Shark (*Hexanchus griseus*), which can reach 20 ft (6.1 m) in length, but there is nothing to fear, as they reside in the deep sea. Another abyssal critter is the slimy Gulper Shark (*Centrophorus granulosus*), which has big green eyes to see in the near pitch-darkness of the deep ocean. The Frilled Shark (*Chlamydoselachus anguineus*)—an eel-like shark with a reptilian-like head and pitchfork teeth—is also a part of this order.

The order Echinorhynchiformes was differentiated relatively recently and contains only two species: the deep-sea Bramble Shark (*Echinorhinus brucus*), which has large, thornlike dermal denticles, and the Prickly Shark (*E. cookie*)—a sluggish, poorly known shark with large scales.

Unsurprisingly, the Spiny Dogfish (*Squalus acanthias*) belongs to the dogfish order (Squaliformes). This order is very diverse, ranging from the tiny Dwarf Lanternshark (*Etmopterus perryi*), 8 in (20 cm) in length, to the massive Greenland Shark (*Somniosus microcephalus*), at 23 ft (7 m), which can live for hundreds of years.

The Squalomorphs boast some of the weirdest and most wonderful of all the sharks. For example, the 23 species of angel sharks (order Squatiniformes) look more like batoids than true sharks and the remarkable sawsharks (order Pristiophoriformes) all sport a strange toothed rostrum that sticks out the front of their face.

Galeomorph sharks

In contrast to the squalomorphs, all the galeomorph sharks possess an anal fin as well as two well-developed dorsal fins that lack spines (except in the horn sharks). Evidence of galeomorph sharks in the fossil record dates to between 310 and 240 MYA, hence they are a more recent group than the squalomorphs. They mostly have highly protrusible jaws, an evolutionary advancement that enables a larger gape and a wider range of prey. While most species live in warmer climates, they are a diverse group, with about 367 species in as many as 24 families, separated into four orders:

Heterodontiformes (bullhead or horn sharks)

Orectolobiformes (carpet sharks)

Lamniformes (mackerel sharks)

Carcharhiniformes (ground or requiem sharks)

A major difference among the galeomorphs is the morphology of their snouts. One assemblage (around 50 species), including the horn sharks (family Heterodontidae), wobbegongs (family Orectolobidae), bamboo sharks (family Hemiscylliidae), nurse sharks (family Ginglymostomatidae), and the Whale Shark (*Rhincodon typus*), possess short snouts and no expanded rostral cartilage. The second group, which includes all of the requiem sharks (family Carcharhinidae) and the mackerel sharks, such as the White Shark, Basking Shark (*Cetorhinus maximus*), Sand Tiger (*Carcharias taurus*), Goblin Shark (*Mitsukurina owstoni*), the thresher sharks (family Alopiidae), and the mako sharks (*Isurus* species), all have elongated rostral cartilage and larger snouts. Additionally, only sharks in the orders Carcharhiniformes and Orectolobiformes have a nictitating membrane (or third eyelid). Also found in frogs, birds, and a few mammals, this clear, thin membrane slides across the eyeball to protect the eye.

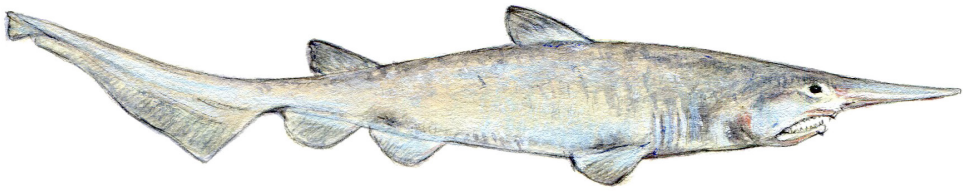
Galeomorphs span the size spectrum, from small demersal (bottom-associated) sharks like the Smallspotted Catshark to the biggest fish in the ocean—the enormous Whale Shark. Despite reaching sizes up to 59 ft (18 m), Whale Sharks feed only on small plankton. Similarly, the second largest shark—the Basking Shark, which can reach 26 ft (7.9 m)—is also a filter-feeder.

Some galeomorphs, like Bull Sharks (*Carcharhinus leucas*) and Tiger Sharks, are voracious predators, while others, such as Nurse Sharks (*Ginglymostoma cirratum*), are more sedate and placid. These bottom-dwelling sharks use a suck-crush-spit-repeat feeding method on their hard-bodied prey (see page 92). The galeomorph group also includes the previously mentioned “walking shark”—the Halmahera Epaulette Shark (*Hemiscyllium halmahera*)—and Sand Tigers, who will feature prominently in Chapter 5.

Not to be outdone by the squalomorph gang, the galeomorphs also boast some truly spectacular oddballs, such as the Common Thresher Shark (*Alopias*

vulpinus), which uses its long tail as a whip while hunting; the Goblin Shark, which can slingshot its entire jaw out of its mouth to increase its reach; and the flabby Megamouth Shark (*Megachasma pelagios*), a rarely encountered, deep-sea plankton-eater. Some of the strangest looking sharks in this group are the bull-head sharks (Heterodontiformes), such as the Port Jackson Shark (*Heterodontus portusjacksoni*), which are so named for their unmistakable, protruding brows. Believe it or not, these little sharks have been trained to recognize jazz music!

The galeomorphs also have some batoid-like sharks in their midst: the wobbegongs. While these sharks share the beautiful skin patterns of their carpet shark cousins (order Orectolobiformes), they look very different. With a flattened body and bizarre, undulating projections around their face that look like a beard, these sharks camouflage perfectly against rocks and corals, which allows them to ambush their prey.



32 in 
95 cm 



7 in 
20 cm 

TWO SPECIES OF GALEOMORPH SHARK

The Goblin Shark (top) and Ornate Wobbegong are more obscure representatives of this group that includes the reef sharks.

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